PRETORIUS, ETHERESIA

PHYLOGENETIC AND MORPHOMETRIC STUDIES OF MAJOR INTERNAL ORGAN SYSTEMS OF THE SCARABAEOIDEA (COLEOPTERA)

PhD (ENTOMOLOGY) UP 1998

PHYLOGENETIC AND MORPHOMETRIC STUDIES OF MAJOR INTERNAL ORGAN SYSTEMS OF THE SCARABAEOIDEA (COLEOPTERA)

by

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SUBMITTED IN PARTIAL FULFILMENT OF THE REQUIREMENTS OF PHILOSOPHIAE DOCTOR: ENTOMOLOGY

DEPARTMENT: ZOOLOGY AND ENTOMOLOGY

in the

FACULTY OF BIOLOGICAL AND AGRICULTURAL SCIENCES
UNIVERSITY OF PRETORIA
PRETORIA

December 1998

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ABSTRACT

Section 1: Detailed descriptions of the alimentary canal, nervous system, male and female reproductive organs and ovipositor morphology of all 13 scarabaeoid families and most subfamilies are presented. Because no organ systems or ovipositor groundplan exists, one was constructed from literature (pertaining to all Insecta, with special reference to Coleoptera and Scarabaeoidea) as well as personal observation of the changes in morphology of the characters. Character states from these systems are not stable, sometimes varying considerably between species of the same genus. Because of this variability, only 18 stable characters were identified. A branch-and-bound cladistic analysis (using PAUP/Mac version 3.1.2d5) was performed, followed by a strict consensus, and a 50% majority rule consensus (on all 18 characters). It was, however, decided to choose only the parsimony-informative characters (totaling 10) and again to perform a branch-and-bound search. This yielded 54 trees and 12 steps. A 50% majority rule consensus was then performed, and this tree chosen as representing the phylogeny of the organ systems and ovipositor. Although only 10 characters identified proved to be parsimony-informative, the 50% majority consensus tree is not totally different to that of the tree proposed by Browne and Scholtz (in press).

Section 2: Geometric morphometric analyses of 12 families belonging to the Scarabaeoidea, using landmarks from three two-dimensional views (frontal, dorsal and lateral) of the metendosternite were done. The metendosternite is one of the internally situated anatomical structures that has largely been neglected in past studies. It, however, proved to be very useful in geometric morphometric studies, because of its rigidness. Procrustes distance matrices were obtained to produce phenograms, relative warp analyses were performed and the results of the first two relative warps (for each of the data sets) plotted against one another. The most landmarks (totaling 19) were identified on the lateral view, and this phenogram also corresponds best with the cladogram of Browne and Scholtz (in press). Geometric morphometrics is a powerful tool that can be used successfully to identify phenetic relationships between higher level taxa, and the metendosternite a new "tool" in the tool box of beetle systematists.

KEYWORDS: [Coleoptera; Scarabaeoidea; internal organs; ovipositor; cladistic analysis; metendosternite; landmarks; geometric morphometrics; thin-plate spline; Procrustes distance].

ACKNOWLEDGEMENTS

This thesis is dedicated to the five most important people in my life, my loving husband Nico, my two sons Carel and Jan-Hendrik, and my dearest grandmother and grandfather. I would like to thank Nico for the hours spent looking after the children, his patience, support, as well as the time spent trying to explain mathematics to me. I would like to thank my children for their patience when they wanted to play with me but could not, as mommy was once again in front of the computer. To my grandmother and dearly departed grandfather, for your love and support and for believing in me.

I would also like to thank my favourite professor, Clarke Scholtz. Thank you for all the long hours spent editing the thesis, your support, kindness and guidance throughout the years. Without you this would not have been possible.

I am also indebted to the following people who have contributed to this thesis:
Prof James Rohlf, Prof Marco Corti, Prof Fred Bookstein, Dr Paulette Bloomer, Dr Chris Chimimba, Dr Nico Dippenaar, and people all over the world who sent scarab beetles to me.

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SECTION 1

Phylogenetic analysis of internal organs (alimentary canal, nervous system, male and female internal reproductive organs and ovipositor) of the Scarabaeoidea

1. BACKGROUND TO STUDY

Introduction

Central to current theory of biological evolution is that species of all organisms originated as modified descendants of other species (Darwin, 1859; Wiley, 1981; Hennig, 1981). This being so, the origin of species belonging to the same groups could theoretically be traced back to a common ancestor if we had all the links (e.g. a complete fossil record) available for study. Undoubtedly, it would be ideal if we could take a particular species from an earlier period of the geological past and describe the history of its descendants right down to the present by means of an uninterrupted series of fossils. Of course that is not available, because of the incompleteness of the fossil record and the general poor state of preservation of most fossil specimens.

After the basic theories behind evolution were established (Darwin, 1859), scientists began to investigate ways to determine the phylogeny (or the genealogical history) of the organisms they studied, and whether a true phylogeny of the organisms could be reconstructed. Variations in the morphology and anatomy of living species and also fossils, describing changes in behaviour, physiology, mode of life and ecology and geographical distribution are different tools utilised to determine the relationship between them. There were, however, few developments in systematic theory until the 1950's.

Hennig (1950) laid down the main goals and principles of cladistic classification, but without describing the actual way to go about reconstructing phylogenetic relationships. He, however, introduced a strict concept of monophyly and general terms like apomorphic, plesiomorphic and character states.

Evolutionary (phylogenetic) systematics developed from the philosophy of phylogeny. During the 1950s two new approaches to systematics developed, phenetics (where species are clustered according to their overall morphometric similarities) and cladistics (relationships are inferred from the extent to which different species share evolutionarily modified features apparently derived from common ancestors). Phenetics aims to determine the relative levels of similarities between species by measurements of characters (e.g. limb length, number of

teeth etc.). Because of the quantitative methods involved, phenetics is sometimes referred to as numerical taxonomy (Wiley, 1981). Evolutionary or phylogenetic relationships are not explicitly sought after, but they are nevertheless supposed to be reflected in phenetic classifications (Skelton, 1993). From the measurements a phenogram is constructed. A phenogram is, however, no more than a hierarchy of relative phenotypic similarity of a set of species. Because of strong criticism against the lack of subjectivity in phenetic procedures, it has not been used in phylogenetics.

Cladistics, however, has emerged in recent years as the most powerful and widely used method of phylogenetic analysis. According to Hennig (considered to be the father of cladistics) and the theory behind cladistics, the natural taxonomy should reflect the phylogeny, and related species should strictly be grouped according to monophyly. Phylogenetic systematics investigates the relationship between all existing species and expresses the results in a form that cannot be misunderstood. Its aim is also to discover the appropriate degrees of phylogenetic relationship within a group of organisms (Hennig, 1981).

Over the years, various authors have been advocating different concepts and definitions regarding taxonomy and phylogenetic systematics. Taxonomy has been categorised into e.g. Linnaean taxonomy, evolutionary taxonomy, Hennigian taxonomy and cladistic taxonomy. Linnaean taxonomy attempts to distinguish the important stable and essential properties from the unimportant variable and nonessential properties (Linnaeus, 1735; Christoffersen, 1995). In evolutionary taxonomy, species are defined as evolutionary units, combining phenetic, patristic and cladistic data into a single taxonomic system (Mayr 1942; Simpson, 1961). Hennigian taxonomy uses the principle of common descent at all levels in the taxonomic hierarchy (Hennig, 1950, 1981). Cladistic taxonomy uses a cladogram as graphical model for constructing a biological system (Nelson, 1978; Nelson & Platnick, 1981; Patterson, 1982, 1983; Farris, 1982 and Maddison *et al.*, 1984).

The theory of phylogenetic systematics was developed partly as a generalisation from taxonomy (Patterson, 1983; de Queiroz, 1985). Systematics is broader and also involves more theory than taxonomy and integrates a transformational approach with the taxic perspective of taxonomy (Eldredge, 1979; Rieppel, 1988a). During the last two decades a split has developed within phylogenetic systematics, dividing it into pattern cladistics and

phylogenetic taxonomy. Pattern cladists avoid all assumptions and preconceptions about the process in reconstructing a taxonomy (Nelson, 1978; Rieppel, 1988a) while phylogenetic taxonomists deduce the most useful taxonomic concepts from general evolutionary processes (de Queiroz, 1985).

Each of the above mentioned authors (and numerous others) changed or added information to the broad concept of phylogeny and systematics and created an interacting network of multifarious, overlapping and sometimes confusing terminology. Luckily, because of the expansion and development of the theory behind evolution, these definitions and concepts are used to reconstruct phylogenies of the animals and plants. In the construction of a cladogram and reconstruction of a phylogeny, I, however, suggest a combination of the cladistic and phylogenetic definitions of Hennig (1950, 1981), Wiley (1981) and Mayr & Ashlock (1991).

In order to reconstruct a phylogeny and to construct a cladogram, characters are needed. Many biologists have attempted, since Hennig to define the term character. Amongst these are:

- Cain & Harrison (1958): "anything that can be considered as a variable independent of any other thing considered at the same time"
- Davis & Heywood (1965): "characters are attributes of organisms that could be adequately described"
- Mayr (1969) used the term taxonomic character and defined it as: "any attribute of a member of a taxon by which it differs or may differ from a member of a different taxon"
- Wiley (1981): "a character is a feature of an organism which is the product of an ontogenetic or cytogenetic sequence of previously existing features, or a feature of a previously existing parental organism(s). Such features arise in evolution by modification of a previously existing ontogenetic or cytogenetic or molecular sequence"

When using morphological characters in determining the phylogeny of a group, certain important facts should be kept in mind (Hennig, 1981):

- The studied species should belong to a monophyletic group.
- Irrespective of rank, every group formation in the phylogenetic system must be established by derivative (apomorphic) characters in its groundplan.

- Where two monophyletic groups (sister groups) together form a monophyletic group, some characters should always appear in a more primitive state (called relative plesiomorph by Hennig, 1981) in one of the two groups.

The question can be asked: why use morphology in determining phylogenetic relationship? The main advantage of studying the morphology of a taxon and using the variation in morphology to produce a phylogeny of the taxon, is that the researcher potentially has available to him, all living species of the taxon (this is theoretically not possible, as not all species of a particular taxon have been collected and described). In most cases more than one specimen per species is also available for study. All major morphological structures (in Entomology) have been used to reconstruct phylogenetic trees, amongst the characters are: mouthparts, antennae, head capsules, legs, wing morphology and external genitalia.

By studying morphological variation, Entomologists have a very good idea of the basic origin and phylogeny of Insecta as well as the different orders within Insecta. Morphological characters used to determine the origin of Insecta (Insecta and Myriapoda form a monophyletic group of higher rank, the Tracheata) were: the intestinal gland (Tiegs & Manton, 1958)); loss of the second antennae (DuPorte, 1957); structure of the pretarsus (Snodgrass, 1958b); morphology of the mandibles (Manton, 1960); musculature of the mandibles and modification of the gnathocepphalon into mandibles and 1st and 2nd maxillae (Siewing, 1960 in Hennig, 1981) and elongation of the intestine and expanded function of the salivary glands (Sharov; 1966b in Hennig 1981). These are but to name a few early studies using morphological characters.

Within Insecta the Coleoptera is known to be a very well defined monophyletic group. Some groundplan characters determined for morphological structures, include the prothoracic connection between the notum, pleura and sternum, the presence of elytra, hindwing structure, morphology of the abdominal segments and morphology of the ovipositor.

The internal organ systems (alimentary canal, nervous system, male and female internal reproductive organs) and ovipositor in Coleoptera have, however, rarely been used in detailed phylogenetic studies. Some of the more in depth of these studies include: Kasap & Crowson (1975) who studied the alimentary canal, reproductive organs and nervous system

of Dascilloidea (six species), Byrrhoidea (eight species), Dryopoidea (24 species), Buprestoidea (10 species), Artematopoidea (six species), Elateroidea (32 species) and Cantharoidea (22 species) (they also examined the abdominal musculature and studied abdominal movements); Tschinkel & Doyen (1980) who studied the female genitalia and defensive glands of 247 species of Tenebrionidae (at least one genus of all the tenebrionid tribes) and Calder (1989 & 1990) who studied the internal organs (alimentary canal, nervous system and male and female reproductive organs) of the Curculionidae.

In this study, morphology of the internal organs and ovipositor of Scarabaeoidea are studied and the phylogenetic and cladistic interpretations of the morphology are then presented. The metendosternite morphology and geometric morphometric analysis of its morphology are presented in Chapter 10 and 11 and will not be discussed further in this chapter. The importance of the morphology of the internal organs of the Scarabaeoidea in analysing their phylogeny was recognised by authors such as Crowson (1938), Ritcher & Baker (1974), Holloway (1972) and Iablokoff-Khnzorian (1977). Ritcher & Baker (1974) studied the variation in ovariole number in 18 subfamilies and many of their tribes. (In this thesis the most recent classification system of the Scarabaeoidea (where the superfamily is classified into 13 families), proposed by Scholtz (1990) and modified by Scholtz & Browne (1996) is followed – discussed later). Holloway (1972) described the morphology and made phylogenetic interpretations of the ovipositor and internal exodermal areas of the female organs of the Diphyllostomatidae, Lucanidae, Trogidae, Glaphyridae, Geotrupidae, Aphodiinae, Scarabaeinae and the Ochodaeinae (as a subfamily of Hybosoridae). Holloway (1960) discussed the female reproductive organs of 11 species of Lucanidae (and systematically revised the New Zealand Lucanidae during 1961). Genera discussed were *Dendroblax*, *Dorcus*, *Lissotes* and *Ceratognathus*. She examined external structures like the eyes and legs, but also form and structure of the female internal genitalia. Iablokoff-Khnzorian (1977), in a comprehensive study of the larvae and adults of the Scarabaeoidea, used external morphology (adults: morphology of the head including the structure of the mandibles, maxillae, labrum and labium, morphology of the thorax and abdomen and wings), as well as internal organ systems (nervous system and male and female reproductive organs) and also the metendosternite, to make phylogenetic deductions.

Detailed taxonomic and ecological studies of a wide variety of taxa in which the morphology

of small numbers of species were compared with each other and brief mention made of the structure of the internal female reproductive organs, are abundant. An example is Zunino (1971) – he briefly mentioned the morphology of the internal female organs of the genus *Onthophagus* (Scarabaeinae) in a taxonomic study. Morphology were also mentioned in ecological studies like Dajoz (1972) – *Scarabaeus semipunctatus*; Halffter & Matthews (1966) and Halffter & Edmonds (1982) – female reproductive organs of the Scarabaeinae; Halffter & Lopez (1977) - *Phanaeus* (Scarabaeinae); Tyndale-Biscoe (1978) - *Euoniticellus intermedius* (Scarabaeinae) and Halffter & Lopez-Guerrero (1985) - *Geotrupes cavicollis* (Geotrupinae).

Various papers merely described the morphology of the internal genitalia of certain species (without including ecological or taxonomic information); some examples are the following: Heymons (1930) – morphology of the female reproductive organs of *Scarabaeus* (Scarabaeinae); Krause (1946) - structure of the gonads of *Passalus cornutus* (Passalidae); Srivastava (1951) - structure of the ovary of *Onitis distinctus* (Scarabaeinae); Mathur & Srivastava (1959) - genitalia of *Oryctes rhinoceros* (Dynastinae); Virkki (1961) - testicular structure of the passalid testis; Berberet & Helms (1972) - anatomy of the alimentary canal, nervous system and male and female reproductive organs of the Melolonthinae species *Phyllophaga anxia*; Baker (1973) - genitalia of three species of the Passalidae genus *Pentalobus*; Reyes-Castillo & Ritcher (1973) - ovariole number in the Passalidae; Edmonds (1974) - internal anatomy of *Coprophanaeus lancifer* (Scarabaeinae); Pluot (1979) - structure of the ovarioles of the Scarabaeinae and Stringer (1990) - structure of the male reproductive organs of *Costelytra zealandica* (Melolonthinae).

There are also numerous published studies on the morphology of the alimentary canal. Some examples are the following: Lewis (1926) - alimentary canal of *Passalus* (Passalidae); Fletcher (1930) - alimentary canal of *Phyllophaga gracilis* (Melolonthinae); Swingle (1930) and Patterson (1937) - alimentary canal of *Passalus cornutus*; Lison (1938) - alimentary canal of *Melolontha melolontha* (Melolonthinae) and Cheung & Low (1975) - midgut of *Protaetia acuminata* (Cetoniinae).

Literature describing the scarabaeoid nervous system includes Cody & Gray (1938) - *Passalus cornutus* and Menees (1961) - *Amphimallon majalis* (Melolonthinae).

Anderson (1950b) described the cytology and cytochemistry of the male accessory glands of the Japanese beetle (*Popillia japonica*), belonging to the Rutelinae.

To date no one has comprehensively studied internal organ systems or the ovipositor of the Scarabaeoidea.

Besides practical reasons of access to sufficient fresh/live study material for comprehensive purposes, the main reason for not using internal organ systems in phylogenetic studies, appears to be that the differences in the morphology of the internal organs are viewed as adaptations (Wiley, 1981; Caveney, 1986). Such organs (for example the alimentary canal) change when the process of evolution takes place if a new selection pressure (for example the sudden change of climate that influences the food source of the animal) is applied. Because of the selection pressure, morphology of the organ changes to meet the demands of this selection pressure. The same selection pressure on a group of organisms may elicit different adaptive responses depending upon the differences in genotypic and phenotypic characteristics of the organisms (Bock, 1965).

It can, therefore, be said that changes in the morphology because of selection pressures are correlated with functional needs and therefore these changes are adaptive. The alimentary canal e.g. changes because of selection pressure and the differences in morphological structure are therefore because of adaptation. The morphology of the internal female and male reproductive organs also change directly because of selection forces on the reproductive capabilities of the animal. But, can one accept that the change in morphology of a structure - when a new selection force (for example the change in climatic conditions) appears is useless in phylogenetic interpretations? I believe that the answer is no: so called "good" phylogenetic characters such as the morphology of the wings, eyes or legs do not perhaps change so "suddenly" as the structure of e.g. the alimentary canal but that does not imply that they are non-adaptive (non-adaptive implies non-functional (Bock, 1965) and these "good" morphological structures are functional).

Another reason for not using these adaptations is that authors believe that it is difficult to identify convergent and homoplasious characters. However, even with "good" phylogenetic

characters it is sometimes difficult to detect convergence or homoplasy. The absolute truth about any hypothesis of homology will never be demonstrated, as the true phylogeny of any group will never be known. When trying to distinguish between homologies and homoplasies, Hennig's auxiliary principle must be kept in mind: "never assume convergent or parallel evolution; always assume homology in the absence of contrary evidence" (Wiley, 1981).

In my view, the lack of phylogenetic interpretations of characters of internal organs of other groups within the Coleoptera and even within Insecta is because researchers believe that internal organs are adaptations and because it is difficult to identify convergent or homoplasious characters.

Why is the aim of this thesis then to determine the phylogeny of the Scarabaeoidea by studying “adaptive characters”? Phylogenetic systematics does not try to classify organisms according to their degree of resemblance, but to their degree of phylogenetic relationship. Hennig’s theories for establishing whether a group of characters should be studied justifies the use of internal organs of the Scarabaeoidea:

- Is the Scarabaeoidea a monophyletic group?
- Can the different ranks to which every group within the Scarabaeoidea belongs be established by apomorphic characters?

Answers to both questions have already been established.

In my opinion the internal organs should be treated as any other morphological structures used in the reconstruction of phylogeny, because each species underwent evolution as a unit – you should therefore treat all morphological characters as equal. You can therefore not ignore the evolution of certain characters because you are of the opinion that they are adaptations, and therefore useless in phylogeny. What I would, however, suggest is that the phylogeny of the internal characters should be compared with those of the traditional “better” morphological structures such as the male external genitalia, wings etc. In doing this, one can then judge the actual value of these structures. This can, however, unfortunately be done only after a study is completed. Before coming to any conclusions (if there are differences in phylogeny) it should be considered very carefully whether the internal organs do not present additional information about the taxon, but from a different angle. Ignoring

internal organs in phylogeny is therefore only turning a blind eye to a potentially very important part of unravelling the ancestor/descendant relationship. Until all morphological structures of a taxon are examined our educated guess about the true origin of this taxon will be incomplete.

THE OBJECTIVES OF THIS PROJECT

A brief description of the objectives of the thesis follows. The objectives can be divided into six main parts:

Section 1 (Chapter 2):

- Brief description and background of the morphology, habits and taxonomy of all families, and in the case of the Scarabaeidae, the different subfamilies.

Section 1 (Chapter 3):

- Background and discussion on the trends regarding Scarabaeoidea phylogeny (including discussions regarding the sistergroup and outgroup of the superfamily).
- Discussions on the available literature on all organ systems and preparation of a groundplan for these organ systems.

Section 1 (Chapters 4 to 8):

- Morphological descriptions of the major internal organ systems, (alimentary canal, nervous system, male and female internal reproductive organs) and ovipositor of members of the 13 families (Browne & Scholtz, 1995; Scholtz & Browne, 1996) of the superfamily Scarabaeoidea and of members of the Polyphaga which are historically believed to be closely related or which have been proposed as outgroups of the Scarabaeoidea; e.g. Hydrophiloidea, Staphylinoidea and Histeroidea (belonging to the Haplogastra proposed by Jeannel & Paulian 1944 – no longer popular, because it is very difficult to substantiate the relationship between the superfamilies based on larval characters), (Crowson, 1955; Paulian, 1988 and Lawrence & Britton, 1991) and also Dascilloidea (Crowson, 1981; Scholtz, 1990). Lawrence & Newton (1982) and Lawrence & Britton (1991), however, do not agree with the Dascilloidea outgroup hypothesis (because of larval habits). Based on the evolution of the hindwing in Coleoptera Kukalová-Peck & Lawrence (1993) support a possible relationship between Haplogastra and Scarabaeoidea and refute a relationship between the Scarabaeoidea and Dascilloidea.

Section 1 (Chapter 9):

- Results from the cladistic analysis of the organ systems as well as the ovipositor

characters, presented as a cladogram.

- Discussion of the results from the cladistic analysis.
- Addressing the following questions:

Are the internal organs and ovipositor useful characters for cladistic analysis?

If they prove useful, does the resulting cladogram confirm or reject relationships indicated in the Browne & Scholtz (in press) cladogram?

Are all the character states of the internal organs and the ovipositor characters present as the most primitive state in the Glaresidae?

Section 2 (Chapter 10):

- Background to geometric morphometric methods and its potential usefulness in this thesis.
- Statistically analyse certain homologous points on three views (frontal, dorsal and lateral views) of the metendosternites called "landmarks" – (*x,y* co-ordinates) by means of geometric morphometrics (geometric morphometrics describes the shape-variability amongst biological structures).
- Construction of a phenogram for each of the three views to determine the shape relationships of the metendosternites amongst the studied groups in the Scarabaeoidea.

Section 2 (Chapter 11):

- Interpret and discuss the results from the phenetic analyses of the metendosternites.

Morphologically, the superfamily Scarabaeoidea is one of the best-studied Coleoptera groups. The reason for this is the many comparative studies covering most of the morphological structures. Other studies, not mentioned in the introduction of this chapter, include research on the morphology of the spiracles (Ritcher, 1969a,b); prothorax (Hlavac, 1975); antennal sensilla (Meinecke, 1975); coxae (Ritcher, 1969c; Hlavac, 1975); antennae (Iablokoff-Khnzorian, 1977); wing morphology (Crowson, 1967; Iablokoff-Khnzorian, 1977); karyotype (Smith & Virkki, 1969) and eyes (Caveney, 1986). Morphology of the larvae was also studied by authors like Areekul (1957), Ritcher (1966) and Hinton (1967). Amongst the recent researchers working to complete the study of the morphological characters are members of the Department of Zoology and Entomology of the University of Pretoria who have worked for a number of years on a project to examine all possible internal and external

characteristics of the Scarabaeoidea. Studies by members of the department include mouthparts (Nel & Scholtz, 1990); male genitalia (d'Hotman & Scholtz, 1990a,b) as well as the hindwing articulation characters (Browne & Scholtz, 1995). Scholtz and co-workers in numerous publications debated the phylogeny and systematics of the superfamily and of individual groups within the superfamily; e.g. phylogeny and systematics of the Trogidae: (Scholtz, 1986); Glaresidae as a new family of Scarabaeoidea (Scholtz *et al.*, 1987) phylogeny and systematics of the Ochodaeidae (Scholtz *et al.*, 1988); the phylogenetic trends of the Scarabaeoidea (Scholtz, 1990); Glaresidae as sistergroup to the rest of the superfamily (Scholtz *et al.*, 1994) and polyphyly of the Geotrupidae (Scholtz & Browne, 1996).

Browne & Scholtz (in press) analysed a total of 134 morphological characters (adults and larvae) cladistically and presented the most comprehensive analysis of the superfamily up to now. Some of the characters of the internal organs and ovipositor investigated in the present study, could perhaps be incorporated in the Browne & Scholtz database in a study to reconstruct the phylogeny for the group that is as close to the true historic phylogeny as possible.

Materials and methods

Materials examined

Members of 13 families of the Scarabaeoidea were studied. The classification system proposed by Scholtz (1990) and modified by Scholtz & Brown (1996) was followed. The primitive lineage comprises Passalidae, Diphyllostomatidae, Lucanidae, Glaresidae, Trogidae, Pleocomidae, Geotrupidae, Bolboceratidae, Glaphyridae, Ochodaeidae, Hybosoridae and Ceratocanthidae. The derived lineage (Scarabaeidae) comprises Aegialiinae, Aulonocneminae, Aphodiinae, Scarabaeinae, Dynastinae, Melolonthinae, Rutelinae, Cetoniinae, Trichiinae and Valginae. Species from the superfamily examined are listed in Appendix 1.1 (at the end of this chapter). (All voucher specimens stored at the Transvaal Museum, Pretoria, South Africa).

Preparation of material for dissection

Material used to study the internal organ systems was either from freshly killed, alcohol preserved, frozen or dried specimens. Live specimens that were not dissected immediately were frozen. Dissecting frozen material proved to be just as successful as dissecting freshly

killed specimens (as long as the specimen is dissected immediately after it is removed from the freezer). The dissection of specimens preserved in alcohol and other preservatives usually proved to be more difficult as the internal organs tended to become brittle. Alcohol preserved specimens were obtained from collectors and co-workers worldwide.

Dissection of specimens longer than about 0.5 cm

Both elytra were removed with forceps after which a small insertion (dorsally) at the point where the thorax joins the abdomen, was made with a pin. A pair of very small dissecting scissors was then inserted into the insertion (care was taken not to pierce the internal organs which are situated close to the dorsal integument) while the insect was held firmly between the thumb and forefinger of the left hand with the abdomen of the insect to the left. The insect must be held firmly as the abdomen otherwise tends to break loose from the thorax. The dorsal integument of the abdomen was then cut open along the middle line to the tip of the abdomen. The pair of scissors was again inserted at the place where the pin was inserted but two cuts were made on the dorsal margins of the thorax towards the head. This "plate" was removed with forceps and this revealed a part of the middle gut and muscles (the plate was removed so as not to force the thorax open when searching for the nervous system which is situated ventrally). The dorsal integument of the head was removed in a v-shape in order to trace the foregut and the sub-oesophageal ganglion of the nervous system.

Dissection of specimens up to about 0.5cm

Specimens up to 0,5cm were dissected with sharp pins (following the same method as above) but without removing the elytra. The elytra were spread out alongside the insect for additional support while dissecting it. The specimen was then pinned open on a piece of wax in a petri dish. To have a clearer view of the internal organs, the specimen was temporarily coloured with azo-black for a few seconds and then with acid-fuchsin, covered with water and examined through a dissecting microscope. Colouring the internal organs was repeated as often as necessary.

The alimentary canal is situated dorsally and was easily pulled loose from the trachea with forceps. The nervous system is situated ventrally in the head and thorax in the more derived groups but in some primitive scarabaeoids, it also stretches as far back as the first or second abdominal segments. The ganglia and connectives of the nervous system are surrounded

by muscles from the wings and legs that must usually be pulled out or cleared away before the delicate structures can be traced.

The posterior end of the chitinous metendosternite is attached on the margin of the thorax and abdomen and stretches anteriorly. The wing and leg muscles are attached to this structure. It was examined only after the nervous system had been removed, as the whole structure must be detached from the insect to examine it laterally. The reproductive organs are situated postero-ventrally under the alimentary canal and are surrounded by trachea.

Dried museum specimens were used to study the ovipositors. The abdomens wereremoved from the dry specimens and softened in boiling water, and then cleared in boiling 10% KOH.

Illustrations of the internal organs and ovipositor were done using a Zeiss dissecting binocular microscope and a Zeiss 1,8 Camera Lucida.

APPENDIX 1.1

PASSALIDAE

FRESHLY KILLED OR PRESERVED SPECIMENS

Subfamily: Passalinae

Leptaulax timorensis

Paxillus macrocerus

Heliscus tropicus

Ogyges marilucasae

Passalus punctiger

Passalidae sp.

Odontotaenius disjunctus

Odontotaenius zodiacus

Subfamily: Aulacocyclinae

Aulacocyclys sp.

DRIED SPECIMENS

Subfamily: Passalinae

Popilius sp.

DIPHYLLOSTOMATIDAE

DRIED SPECIMENS

Diphyllostoma linsleyi

LUCANIDAE

FRESHLY KILLED OR PRESERVED SPECIMENS

Subfamily: Lucaninae

Prosopocoilus natalensis (Cladognathini)

Figulus sp.(Figulini)

Macrodorcus rectus (Dorcini)

Platyceropsis sp. (Platycerini)

Nipponodorcus rubrofemoratus (Dorcini)

Subfamily: Syndesinae

Syndesus cornutus (Sindesini)

Sinodendron rugosum (Sinodendrini)

Ceruchus sp. (Ceruchini)

DRIED SPECIMENS

Subfamily: Lucaninae

Platycerus oregonensis (Platycerini)

Lucanus maculifemoratus

Pseudolucanus mazama

Subfamily: Nicaginae

Ceratognathus sp.

Subfamily: Syndesinae

Ceruchus punctatus (Ceruchini)

Sinodendron cylindricum (Sinodendrini)

Subfamily: Chiasognathinae

Rhyssonotus nebulosus

Cacostomus squamosus

Lucanidae sp.

Lucanidae sp.

GLARESIDAE

FRESHLY KILLED OR PRESERVED SPECIMENS

Glaresis sp. 1

Glaresis sp. 2

TROGIDAE

FRESHLY KILLED OR PRESERVED SPECIMENS

Genus: *Omorgus*

Omorgus asperulatus

Omorgus melancholicus

Omorgus freyi

Omorgus suberosus

Genus: *Trox*

Trox consimilis

Trox sulcatus

Trox squamiger

Trox rhyparoides

Genus: *Polynoncus*

Polynoncus pedestris

DRIED SPECIMENS

Genus: *Omorgus*

Omorgus scutellaris

Omorgus squalidus

Omorgus obesus

Omorgus consanguineus

Omorgus radula

Genus: *Polynoncus*

Polynoncus longitarsis

PLEOCOMIDAE

FRESHLY KILLED OR PRESERVED SPECIMENS

Genus: *Pleocoma*

Pleocoma shostensis

Pleocoma simbriata

Pleocoma richseckeri

Pleocoma sp.

Pleocoma sp.

DRIED SPECIMENS

Genus: *Pleocoma*

Pleocoma dubitabilis

Pleocoma edwardsii

BOLBOCERATIDAE

FRESHLY KILLED OR PRESERVED

Prototrupes copridoides

Bolbocaffer sp.

SPECIES STUDIED (DRIED)

Bolbolaeus truncatus

Elephastomus meraldus

Bolborachium tricavicolle

Bolbocerastes regalis

Bolbocerus obesus

Eucanthus lazarus

Pseudathyreus orientalis

Athyreus bifurcatus

Neoathyreus panamensis

GEOTRUPIDAE

FRESHLY KILLED OR PRESERVED SPECIMENS

Subfamily: Taurocerastinae

Frickius variolosus

Taurocerastes sp.

Subfamily: Geotrupinae

Geotrupes spiniger

Blackburnium ambiguum

SPECIES STUDIED (DRIED)

Subfamily: Geotrupinae

Enoplutrupes bieti

Mycotrupes gagei

Geotrupes splendidus

Geotrupes gautemalensis

Thorectus cheisinus

Subfamily: Lethrinae

Lethrus apterus

Lethrus carinatus

Lethrus pygmaeus

GLAPHYRIDAE

FRESHLY KILLED OR PRESERVED SPECIMENS

Subfamily: Glaphyrinae

Lichnanthe apina

L. rathvoni

L. brachyselis

L. ursina

OCHODAEIDAE

DRIED SPECIMENS

Subfamily: Ochodaeinae

Ochodaeus inarmatus

O. punctatus

O. kansasus

O. repondus

Subfamily: Chaetocanthinae

Chaetocanthus insuetus

Synochodaeus costatus

S. cucullus

HYBOSORIDAE

FRESHLY KILLED OR PRESERVED SPECIMENS

Phaeochrous mashunus

Hybosorus illegri

Liparochrus hackeri

DRIED SPECIMENS

Liparochrus hackeri

Anaides sp.

Coelodus sp.

CERATOCANTHIDAE

FRESHLY KILLED OR PRESERVED

Ceratocanthidae sp. 1

DRIED SPECIMENS

Cloeotus sp.

Chaetodus sp.

APHODIINAE

FRESHLY KILLED OR PRESERVED

Tribe: Aphodiini

Aphodius russatus

Aphodius septemmaculatus

Aphodius impurus

Aphodius sp.

Colobopterus maculecollis

DRIED SPECIMENS

Tribe: Aphodiini

Aphodius tasmaniae

Aphodius bimentarius

Aphodius fossor

Tribe: Eupariini

Ataenius cognatus

SCARABAEINAE

FRESHLY KILLED OR PRESERVED

Tribe: Onthophagini

Onthophagus gazella (*Digitonthophagus gazella*)

Onthophagus sp.

Proagoderus fossidorsis

Phalops sp.

Tribe: Scarabaeini

GYMNOPLEURINA

Garreta nitens

Gymnopleurus sp.

SISYPHINA

Sisyphus sp.

SCARABAEINA

Pachylomerus femoralis

Kheper sp.

CANTHONINA

Anachalcos convexus

Circellium bacchus

Tribe: Onitini

Onitis alexis

Onitis fulgidus

Onitis caffer

Tribe: Coprini

COPRINA

Copris sp.

Coprini sp.

DICHOTOMIINA

Pedaria sp.

Sarophorus sp.

Tribe: Oniticellini

ONITICELLINA

Euoniticellus intermedius

Tribe: Pinotini

Pinotini sp.

Pinotini sp.

DRIED SPECIMENS

Tribe: Scarabaeini

SCARABAEINA

Scarabaeus flavicornis

CANTHONINA

Epirinus validus

Labroma umbratilis

Temnoplectron rotundum

Tribe Coprini

Metacatharsius sp.

Cephalodesmius armiger

COPRINA

Copris sp.

Copris sp.

PHANAEINA

Phanaeus daman

Tribe: Eurysternini

Eurysternus magnus

Tribe: Onthophagini

Diastellopalpus thomsoni

MELOLONTHINAE

FRESHLY KILLED OR PRESERVED

Melolonthinae sp. 1 (Parys: 26.55S; 27.28E)

Melolonthinae sp. 2 (Parys: 26.55S; 27.28E)

Melolonthinae sp. 3 (Kruger National Park - Pafuri: 22.27S; 31.21E)

Melolonthinae sp. 4 (Pretoria: 25.45S; 28.12E)

Melolonthinae sp. 5 (Pretoria: 25.45S; 28.12E)

Melolonthinae sp. 6 (Kalahari)

Melolonthinae sp. 7 (Plettenberg Bay: 34.05S; 23.21E)

Melolonthinae sp. 8 (Richards Bay: 28.45S; 31.45E)

Sparmannia flava

DRIED SPECIMENS

Neoheteronyx cribrifrons

Ptichopus angulatus

Colpochila tindalei

Haplopsis lineoligera

Xylonichus eucalypti

Phyllotocus rufipennis

Schizonycha rugosa

S. puncticollis

Lepiserica sp.

Hypopholis sp.

Allokotarsa sp.

Pleophylla sp.

Serica sp.

Macrodactylus sp.

Phyllophaga fulviventris

Isonychus sp.

Liparetrus sp.

RUTELINAE

FRESHLY KILLED OR PRESERVED

Rutelinae sp. (Pretoria: 25.45S; 28.12E)

Rutelinae sp. (Pretoria: 25.45S; 28.12E)

Rutelinae sp. (Richards Bay: 28.45S; 31.45E)

Rutelinae sp. (Richards Bay: 28.45S; 31.45E)

Rutelinae sp. (Plettenberg Bay: 34.05S; 23.21E)

Anomala testaceipennis

Anomala daimaina

Anomala sp. 1

Anomala sp. 2

Callcodes frenchi

Leptohoplia testocepennis

Pelidnota notata

DRIED SPECIMENS

Anomala neoplondeus

Anomala testaceipennis

Anomala cupricollis

Peritrichia subsquamosa

Adoretus variegatus

Amocrates sp.

Popillia japonica

Paracotalpa sp.

Pelidnota sp.

Stigoderma sp.

HOPLIINAE

FRESHLY KILLED OR PRESERVED

Hopliinae sp. (Pretoria: 25.45S; 28.12E)

Hopliinae sp. (Pretoria: 25.45S; 28.12E)

Hopliinae sp. (Pretoria: 25.45S; 28.12E)

Tribe Pachycnemini

Monochelus sp.

Eriesthes sp.

DRIED SPECIMENS

Tribe Pachycnemini

Pachycnema striata

Scelophysa militaris

Tribe: Hopliini

Hoplia sordita

DYNASTINAE

FRESHLY KILLED OR PRESERVED

Tribe: Phileurini

Dynastes sp.

Tribe: Oryctini

Oryctes boas

Tribe: Pentodontini

Heteronychus arator

DRIED SPECIMENS

Cryptodus paradoxus

Tribe: Pentodontini

Oxygryllius ruginosus

Tribe: Cyclocephalini

Cyclocephala sp.

CETONIINAE

FRESHLY KILLED OR PRESERVED

Tribe: Goliathini

Hypselogenia geotrupina

Eudicella smithii

Tribe: Cetoniini

Raceloma jansoni

Dischista cincta

Leucoscelis haemorrhoidales

Cetonia roelofsi

Anisorrhina flavamaculata

Cetoniini sp.

Tribe: Diplognathini

Diplognatha silicea

Porphyronota maculatissima

Uncertain tribe

Ichnostoma stobbiae

Plaesiorrhinella trivittata

DRIED SPECIMENS

Tribe: Gymnetini

Cotinus mirabilis

Tribe: Cetoniini

Glycyphana stolata

Euphoria sp.

Rhabdotis semipunctata

Tephrala dichroa

Tribe: Cremastochelini

Oplostomus fuliginosus

Genuchus hottentottus

Tribe: Diplognathini

Poecilophila hebraea

Tribe: Schizorhinini

Eupocila australasiae

Aphonesthes gymnopleura

Diaphonia dorsalis

Uncertain tribe

Conastethus impressus

Lamaptera cinnamomea

Polystigma punctatum

VALGINAE

DRIED SPECIMENS

Valgini sp.

FRESHLY KILLED OR PRESERVED

Campulipus limbatus

TRICHIINAE

DRIED SPECIMENS

Trigonopeltastes sallai

Trichius sp.

Gnorimella sp.

ONCERINAE

DRIED SPECIMENS

Oncerus floralis

CHASMATOPTERINAE

DRIED SPECIMENS

Chnaunanthus chapini

ORPHNINAE

DRIED SPECIMENS

Orphnus capensis

2. CLASSIFICATION AND HABITS OF THE SCARABAEOIDEA

Introduction

The Scarabaeoidea is one of the most variable superfamilies in the Coleoptera, consisting of thirteen families (classification and family concepts of Scholtz (1990) and Scholtz & Browne (1996) are followed). Members differ considerably in size and are found in all types of habitats, from rain forests to arid areas. Members of the taxon feed on most types of dung and a wide range of plant and animal matter, e.g. detritus, fungi, carrion, plant tissues (sap, pollen, flowers, leaves etc.) and some members also prey on other insects. Habits vary from free-living to brood-care and sub-social behaviour (Scholtz, 1990; Browne & Scholtz, 1995).

Most adults are robust and short-legged with a lamellate antennal club, a modified prothorax with large coxae (lacking hind coxal plates), dentate tibiae, an intrinsic wing-folding mechanism, second abdominal sternite represented only by a lateral portion, the 8th tergite forming a pygidium, and four Malpighian tubules (Browne & Scholtz, 1995). The usually C-shaped larvae are grub-like with well-developed antennae and legs, but without urogomphi.

Members of the Scarabaeoidea are morphologically well-studied and monophyly of the superfamily is undisputed (Lawrence and Britton, 1991). Over the past 20 years several comparative studies of most of the major anatomical structures have been undertaken (reviewed in Scholtz 1990, and Browne and Scholtz 1995 - who proposed a phylogeny of the superfamily based on characters of the hindwing articulation, hindwing base and wing venetation) but with the exception of a partial phylogenetic analysis of some of the major groups by Howden (1982), the only comprehensive phylogenetic analysis undertaken was a recent one by Browne and Scholtz (in press).

In the past the Scarabaeoidea have been divided into three categories, primitive, intermediate and derived groups. Browne & Scholtz (1995) used a different hierarchical system to name the different components of the phylogram they reconstructed from the hindwing articulation and hindwing base characters, namely: lineage, line, group, subgroup and infragroup. When these comprise more that one terminal taxon, they are named for the most primitive included taxon.

Authors commenting on individual taxa within the Scarabaeoidea are: Scholtz (1982, 1983) and Browne (1991a) - Glaresidae; Reyes-Castillo (1970) - Passalidae; Brinck (1956), Holloway (1960, 1969), Howden & Lawrence (1974), Lawrence (1981), and Ratcliffe (1984)- Lucanidae; Holloway (1972) - Diphyllostomatidae; Hinton (1967), Holloway (1972) and Zunino (1988) - Glaphyridae; Arrow (1912), Gordon (1970), Smith & Virkki (1979); Scholtz (1986) and Scholtz & Peck (1990) - Trogidae; Browne (1991a,b) and Scholtz & Browne (1996) - Bolboceratidae; Browne (1991a) - Pleocomidae; Howden (1955), Zunino (1984), Howden & Peck (1987) and Browne (1991a) - Geotrupidae; Howden & Gill (1988) - Hybosoridae; Iablokoff-Khnzorian (1977) and Howden & Gill (1988) - Ceratocanthidae; Carlson & Ritcher (1974), Iablokoff-Khnzorian (1977) and Scholtz *et al.* (1988) - Ochodaeidae; Schmidt (1922). Authors commenting on the subfamilies of the Scarabaeidae are: Tangeleder & Krikken (1982), Stebnicka (1985) and Cambefort (1987) - Aphodiinae; Halffter & Edmonds (1982), Zunino (1983) and Howden (1988) - Scarabaeinae; Machatschke (1959), Meinecke (1975), Yadav & Pillai (1976), Howden (1988) and Lawrence & Britton (1991) - Melolonthinae; Meinecke (1975) - Rutelinae; Hardy (1977) - Hopliinae; Meinecke (1975) and Krikken (1984) - Cetoniinae; Leng (1920), Blackwelder (1944), Howden (1968) and Krikken (1984) - Trichiinae; Krikken (1978, 1984) - Valginae; Leng (1920) and Saylor (1938) - Oncerinae; Saylor (1938) - Chasmatopterinae and Paulian & Lumaret (1984) - Orphninae.

The aims of this chapter are to:

- Give a general, but brief introduction (where the taxon occurs, general morphology and adult and larval habits) to each taxon (family, or subfamily in the case of the Scarabaeidae).
- Discuss different views of authors in connection with the phylogenetic placement ofthe families and subfamilies within the Scarabaeoidea.

Glaresidae

This group, consisting of very small (between 2,5 and 6 mm long), light buff to dark brown beetles, occurs in sandy and arid regions of the world (but absent from Australia). It is thought that the adults feed on organic debris in the ground (Scholtz – personal communication) but unfortunately very little is known about their biology (Scholtz *et al.*, 1994; Scholtz *et al.*, 1987). Nothing is known about the larvae.

This family, consisting of only one genus *Glaresis* Erichson and approximately 50 species world-wide, was originally placed in the Trogidae (Arrow, 1912; Scholtz, 1982,1983) or as a member of the Troginae in the Scarabaeidae (Gordon, 1970). Scholtz *et al.* (1987) did not find any demonstrable apomorphies which the genus *Glaresis* shares with any member of the superfamily and consequently proposed the family Glaresidae. It is believed that Glaresidae is the most primitive living member of Scarabaeoidea (Smith & Virkki, 1979; d'Hotman & Scholtz, 1990b; Nel & Scholtz, 1990; Scholtz, 1990; Browne, 1991a, 1993; Scholtz, *et al.*, 1994; Browne & Scholtz, 1995).

Scholtz *et al.* (1994) presented evidence that the family Glaresidae represents the sistergroup of the rest of the Scarabaeoidea. This was based on the analysis of states of 43 morphological characters. A phylogenetic analysis done by Browne & Scholtz (1995) indicated that there are two basal lineages within the Scarabaeoidea, the glaresid lineage (with only Glaresidae) and the second the passalid-scarabaeid lineage. The study indicated that the glaresid lineage is the sistergroup of the rest of the superfamily (or passalid-scarabaeid lineage). This was reiterated by Browne & Scholtz (in press). The glaresid lineage does not display any autapomorphic characters of the hindwing articulation or wing base, but displays two autapomorphic characters of the wing venetation Browne & Scholtz (1995).

Passalidae

Adult members of this family are usually large, elongated, flattened beetles with distinctly striated elytra. The antennae are curved and the different segments of the antennal club do not fit close together. Larvae are not typically C-shaped (as most other members of the superfamily) and their hindlegs are reduced to stumps. Passalidae is a widespread family, and although present in temperate areas, is essentially a tropical family. There are approximately 40 genera and 500 species (Reyes-Castillo, 1970). Only one species, *Didimus sansibaricus* occurs in the north-eastern parts of southern Africa (Scholtz & Holm, 1985).

Adults as well as larvae are found in decaying hardwood logs and live in small family groups consisting of a few individuals. Adults feed the larvae on prepared stomodeal food (Reyes-

Castillo & Halffter, 1984).

This family is divided into two subfamilies, the primitive Aulacocyclinae and derived Passalinae (Reyes-Castillo, 1970). Passalidae is one of the primitive Scarabaeoidea families (Crowson, 1967, 1981; Reyes-Castillo, 1970; Howden, 1982; Scholtz, 1990; Browne & Scholtz, 1995) and has some characteristics that are not typically found in the superfamily. Amongst these are maxillary palpi possessing two segments, an unusual aedeagus (it has a spherical appearance and unusually sclerotised - it has undergone reduction in lateral sclerotization and the dorsal aspect is membranous (d' Hotman & Scholtz, 1990)) and an elongated larval shape (Scholtz, 1990).

On the basis of wing, wingbase and wing articulation characters, Browne & Scholtz (1995) placed Passalidae as the most primitive member within the passalid line. The remaining members of the passalid line, the lucanid and glaphyrid groups form the sistergroup of the Passalidae. The remaining members of the passalid lineage are Diphyllostomatidae, Lucanidae, Glaphyridae, Trogidae, Pleocomidae and Bolboceratidae.

Lucanidae

Members of the Lucanidae are known as stag beetles, and are usually moderate to large beetles (15 - 35 mm), and brown or black with prognathous heads and large mandibles. Their antennae are elbowed and the segments of the club cannot be held together. There are winged as well as apterous species within the family.

The family Lucanidae consists of about 1000 species (included in approximately 100 genera), found widespread over the world (Scholtz, 1990). Southern Africa, however, has a relatively poor lucanid fauna. There are 22 species known from southern Africa in four subfamilies and six genera. Adults as well as larvae are found under bark in rotting wood, sometimes occurring together (Scholtz, 1990). Occasionally adults visit flowers. Larvae are sometimes found in soil and are soil/humus-feeding (Scholtz & Endrödy -Younga, 1994).

There is little agreement amongst authors on lucanid classification. Number of subfamilies, and tribes, as well as phylogenetic relationships, particularly in the case of the more primitive groups are debated by the different authors (Brinck, 1956; Holloway, 1960; 1969; Howden &

Lawrence, 1974; Lawrence, 1981; Ratcliffe, 1984). At present six subfamilies are recognised (see Scholtz, 1990): the primitive Aesalinae, Nicaginae and Syndesinae, the intermediate Lampriminae and the derived Lucaninae and Penichrolucaninae.

It is accepted that the family belongs to the primitive Scarabaeoidea. However, there is disagreement amongst authors of the exact position the family occupies within the primitive Scarabaeoidea. Sharp and Muir (1912) suggested a relationship between Lucanidae and Trogidae because of the similarity of the aedeagus. Crowson (1967) suggested a relationship between Geotrupidae and Lucanidae because of the similarity between the stridulating mechanism of the larval legs of the two groups. The acone ommatidium structure of the lucanids is also similar to that of the Diphyllostomatidae (Caveney, 1986; Scholtz, 1990). Howden (1982) considered lucanids to be most closely related to Passalidae, and that Lucanidae branched off early from the passalid lineage, following a separate evolutionary pathway.

Wing articulation and wing base characters, however, do not support Howden's (1982) proposal. Browne (thesis: 1993) suggested that Lucanidae is the derived sistergroup of Diphyllostomatidae. Browne & Scholtz (1995) placed Lucanidae in the passalid line. Lucanidae, together with Diphyllostomatidae form the lucanid group (Browne & Scholtz, 1995).

Diphyllostomatidae

Members of the family Diphyllostomatidae are dimorphic (winged males and wingless females, with the eyes and antenna reduced) and endemic to the western USA. Three species have been described in this family. Very little is known about their biology, and no larvae have been found.

Diphyllostoma (the only genus) was previously treated as a member of the Lucanidae (belonging to the subfamily Aesalinae) based mainly on the exposed second abdominal segment, reduced female genitalia, male genitalia, wing venetation, and presence of exposed protrochantin, but Holloway (1972) elevated the genus to family status. This group is believed to be one of the more primitive members of the Scarabaeoidea (Scholtz, 1990). There is, however, speculation about the exact placement of the Diphyllostomatidae within

the superfamily. Holloway (1972) suggested (on the basis of the structure of the female ovipositor and other morphological characters) that the family is more closely related to the Geotrupidae. Caveney (1986) and d'Hotman & Scholtz (1990b) presented strong evidence that Diphyllostomatidae is probably more closely related to Lucanidae than to Geotrupidae. Recently Browne & Scholtz (1995), on the basis of wing articulation and wing base characters, placed the family in the passalid line and suggested that it is the primitive sistergroup of Lucanidae.

Glaphyridae

Members of the Glaphyridae are long-legged, hairy and sometimes brightly coloured (Crowson, 1967). This family contains two subfamilies, Lichniinae, which are only found in South America and Glaphyrinae, which are found widespread in the Holarctic Region. Adults often visit flowers. The males of species belonging to *Amphicoma* feed on pollen while adults of *Lichnanthe* never feed (Ritcher, 1958). Larvae feed on roots, decaying leaves and plant debris (Ritcher, 1958).

The position of the family within the Scarabaeoidea has long been debated. Hinton (1967) suggested family status to this group, but Zunino (1988) suggested that the family is phylogenetically situated between Melolonthinae and Scarabaeinae. Crowson (1967) suggested Glaphyridae to be close to Diphyllostomatidae. Holloway (1972) was unable to find evidence for this placement. d'Hotman & Scholtz (1990a,b; Scholtz, 1990) found that the family is primitive and that the basal piece of the male genitalia is very similar to that of some lucanid genera. Browne (thesis: 1993) suggested, on the basis of wing articulation features, that Glaphyridae occupies an intermediate position between Diphyllostomatidae + Lucanidae and Trogidae, therefore placed as a member of the "primitive" Scarabaeoidea.

Browne & Scholtz (1995) placed Glaphyridae as the glaphyrid group (containing Glaphyridae and the trogid subgroup) in the passalid line of the passalid lineage. Glaphyridae is therefore the sistergroup of the trogid subgroup which contains Trogidae, Bolboceratidae and Pleocomidae. The Browne and Scholtz (in press) analysis indicated that the Glaphyridae is the sistergroup of the trogid + bolboceratid group.

Trogidae

Trogidae is a small, distinctive cosmopolitan family, consisting of approximately 300 species (Scholtz, 1986). Most species occur in arid regions of the southern continents. Adults as well as larvae can be present on any type of animal remains and feed mainly on keratin (but have been found feeding on bat guano, locust eggs and maggots) (Scholtz, 1986). They are usually among the last animals that occur on carcasses. Members of the family are small to moderate (5 - 21 mm), robust, grey-black beetles. The beetles are easily recognised by their sculptured elytra consisting of tubercles and ridges. The head is usually deflexed and concealed from above, while the legs are retractile. When handled, the adults stridulate by rubbing a ridge on the penultimate abdominal tergite on a ridge on the inner margins of the elytra. The adults possess antennae with 10 segments (3-jointed club) (Scholtz, 1986, Scholtz 1990, Scholtz & Peck, 1990).

The larvae are white with a dark head capsule and possess three pairs of well developed legs with prominent claws. They form vertical tunnels in the soil beneath the food source.

This well-defined family consists of three genera, *Trox* Fabricius (occurring in Europe, North America and Africa), *Omorgus* Erichson (occurring in South- and North America, Australia and Africa) and *Polynoncus* Burmeister (occurring only in South America) (Scholtz, 1986). The family comprises two lineages, the primitive *Trox* lineage and a derived *Polynoncus* and *Omorgus* lineage (Scholtz, 1986; Scholtz & Peck 1990). *Omorgus* is considered to be more derived than *Polynoncus*. It is believed that the family is one of the primitive Scarabaeoidea (Crowson, 1967, 1981; Scholtz, 1986). Howden (1982) suggested that the family is highly derived and closely related to the Hybosoridae, while Browne (thesis: 1993) concluded that the Trogidae occupy an intermediate position between Glaphyridae, Pleocomidae and Bolboceratidae. According to analysis of the hindwing articulation, hindwing base and wing venetation, Trogidae is in the glaphyrid group (containing Glaphyridae, Trogidae, Bolboceratidae and Pleocomidae) of the passalid lineage (Browne & Scholtz, 1995). The glaphyrid group is further subdivided into Glaphyridae and the trogid subgroup (containing Trogidae, Bolboceratidae and Pleocomidae). Trogidae occupies an intermediate position between Glaphyridae and the bolboceratid infragroup (containing Bolboceratidae and Pleocomidae). The Browne & Scholtz (in press) analysis indicated that the Trogidae is the sistergroup of the passalid subgroup.

Bolboceratidae

Bolboceratidae is a cosmopolitan family (found in the Nearctic, Neotropical and Australian regions and in Africa) with about 40 genera and 400 species (are richest in Australia - about half of the world fauna is found in this region). Adults are diurnal, nocturnal or crepuscular, and attracted to light. Adults burrow, the entrance being marked by a "push-up" of dirt and feed on fungi and detritus, some adults, however, do not feed (e.g. members of*Eucanthus*) (Howden, 1982; Howden & Cooper, 1977). Larvae are found in burrows formed by adults.

Members of the family Bolboceratidae were previously included as a subfamily of the family Geotrupidae mainly by the fact that they have 11-segmented antennae. The 11-segmented antennal condition is, however, regarded as primitive and therefore carries little phylogenetic weight (Scholtz *et al.*, 1994). Howden (1982) placed the taxon (Bolboceratini as a tribe of the Geotrupinae) in the Scarabaeidae, because of two synapomorphic characters - detritus-feeding and larval burrows formed by the adults. These habits are, however, widespread in the Scarabaeoidea (Scholtz & Browne, 1996) and on their own, not very good characters to base phylogenetic placement on. Zunino (1984a) also regarded the taxon as a subfamily of the Geotrupidae, and the Geotrupidae as closely related to the Pleocomidae.

Scholtz (1990), Browne (1991a, 1993) and Scholtz *et al.* (1994) indicated that in the Geotrupidae there are two distinctly identifiable and unrelated groups, the Bolboceratinae group and the Geotrupinae, Lethrinae and Taurocerastinae group. Scholtz & Browne (1996) concluded, after a comprehensive cladistic analysis of all characters available (antenna, antennal sensilla, ommatidium structure, mandibles, mesothoracic and abdominal spiracles, intersegmentalia, aedeagus, karyotype, hypopharynx, abdominal apex, hindwing articulation, hindwing base and wing venetation) that the Geotrupidae is polyphyletic, and that it can be divided into two distinct unrelated groups, the "Bolboceratinae" and the Geotrupinae, Lethrinae and Taurocerastinae cluster. From the analysis of the different characters, Scholtz & Browne (1996) thereby proposed that the Bolboceratinae be elevated to Bolboceratidae.

This taxon belongs to the primitive Scarabaeoidea (Scholtz, 1990; Browne, 1991a,b). On the basis of wing articulation characters, Browne (thesis: 1993) identified two lineages, a primitive *Eucanthus* lineage and a derived Bolboceratini + Athyreini lineage. Scholtz & Browne (1996) presently consider "Athyreini" as a distinct group within the Bolboceratidae.

Browne (thesis: 1993) suggests that Bolboceratidae is a sistergroup of Pleocomidae. Browne & Scholtz (1995) placed the Bolboceratidae in the glaphyrid group of the passalid lineage. The glaphyrid group consists of the trogid subgroup (containing Trogidae, Bolboceratidae and Pleocomidae). The trogid subgroup is further divided into the Trogidae and the bolboceratid infragroup (containing Bolboceratidae and Pleocomidae). Browne & Scholtz (1995 and in press) reiterated Browne's (thesis: 1993) findings that Bolboceratidae is the sistergroup of Pleocomidae.

Pleocomidae

The family Pleocomidae (also known as rainbeetles, because they tend to fly just before or during the winter rains) is a monotypical family, consisting of one genus, *Pleocoma* Le Conte, with approximately 33 described species and 3 subspecies (Hovore, 1977) and is restricted to western North America. Adults of this family do not feed, while the larvae (which are long-lived - up to as long as between 8 and 13 years {personal communication, Frank Hovore}) feed on roots of a variety of shrubs, trees and sometimes grass and are adapted for burrowing (Scholtz ,1990). Adults are dimorphic (males winged and females wingless).

Because members of the taxon *Pleocoma* possess 11-segmented antennae, they were previously placed in the Geotrupidae (Paulian, 1941). The genus *Pleocoma* is presently treated as the sole representative of the monotypic family Pleocomidae (Crowson, 1981; Lawrence & Newton, 1982; Scholtz, 1990) because the antennal segment number within the Scarabaeoidea is very variable and the 11-segmented condition is usually considered to be primitive and therefore carries little phylogenetic significance (and is regarded as a symplesiomorphic character) (Scholtz *et al.*, 1994; Scholtz & Browne, 1996). It is, however, believed that members of the Pleocomidae are closely related to Geotrupidae (Ritcher, 1966). It has also been suggested that the Pleocomidae may be related tot he Melolonthinae (Howden, 1982), due to the highly modified club with four – seven annuli..

Pleocomidae share genitalic and mouthpart characters with Diphyllostomatidae, but more derived characters with Geotrupidae (d'Hotman & Scholtz, 1990b; Nel & Scholtz 1990; Scholtz, 1990). Pleocomidae and Geotrupidae have similar spiracles (Ritcher, 1969a) and eye structure (Caveney, 1986). Browne (1991a; thesis: 1993) suggested, on the basis of

wing articulation characters that the family is a sistergroup of Bolboceratidae. According to Browne & Scholtz (1995) Pleocomidae is situated in the glaphyrid group (together with Glaphyridae, Trogidae and Bolboceratidae) of the passalid lineage. The trogid subgroup of the glaphyrid group contains Trogidae and the bolboceratid infragroup (containing the two families Pleocomidae and Bolboceratidae). The Browne & Scholtz (in press) analysis also indicated a close relationship between Pleocomidae and Bolboceratidae.

Geotrupidae

Members of the Geotrupidae are medium-sized (10 - 25 mm), convex and stout beetles. Species collect deer and cattle dung which they bury (in much the same way as members of the Scarabaeinae) and on which the adults and larvae feed. The larvae are typically scarabaeoid but have the third pair of legs reduced. Members of this family have brood burrows for the larvae with the adults providing the necessary food for the young (Scholtz, 1990).

Geotrupidae is a widespread family comprising three subfamilies, Geotrupinae - approximately 25 genera and 130 species (mainly Holarctic), Lethrinae - consisting of a single genus *Lethrus* which has 90 species (mainly Angarian) and Taurocerastinae (Sub-antarctic Patagonian) - consisting of two genera and three species (Neotropical Region) (Howden & Peck, 1987; Iablokoff-Khnzorian, 1977; Zunino, 1984). Geotrupidae have traditionally been united mainly by the fact that most of the taxa have 11-segmented antennae (except members of the Taurocerastinae which have 10-segmented antennae).

Geotrupidae is a well-studied family as many authors looked at a wide range of characters. Characters studied were: larval, abdominal and thoracic spiracular characters (Ritcher 1969a,b); ovariole numbers (Ritcher & Baker, 1974); karyotypes (Yadav & Pillai, 1976); eye structure (Caveney, 1986); male genitalia (d'Hotman & Scholtz, 1990); adult mouthpart structure (Nel & Scholtz, 1990); wing articulation sclerites and wing base structure (Browne, 1991a, 1993).

Geotrupidae is a member of the intermediate scarabaeoid lineage, (Howden, 1982; Scholtz, 1990; Browne, 1991) and a sistergroup of Hybosoridae + Ochodaeidae + Ceratocanthidae (Browne, thesis: 1993) According to Howden (1955) as well as Zunino (1984) the taxon is

closely related to Pleocomidae.

Browne & Scholtz (1995) placed Geotrupidae in the geotrupid line (containing Geotrupidae, Ochodaeidae, Ceratocanthidae and Hybosoridae) of the passalid lineage. The geotrupid line is further divided into Geotrupidae (the most primitive family within the geotrupid line) and the ochodaeid group - the sistergroup of the Geotrupidae.

Ochodaeidae

This is a small family, virtually cosmopolitan in distribution (excluding Australia). The family comprises eight genera and about 80 species. The largest genus *Ochodaeus* is found in North and South America, Africa, Madagascar, Europe the Orient and a number of oriental and Palaearctic Islands. The other genera comprise few species or are monotypic and have a restricted distribution (Scholtz *et al.*, 1988). Most species occur in sandy, arid areas. Very little is known about the biology of this family, but they are nocturnal, attracted to light, and burrow in the soil (Carlson & Ritcher, 1974). Little is also known about the feeding habits of these beetles. Members of *Pseudochodaeus* feed on fungi spores (Carlson & Ritcher, 1974). It is thought that the larvae are subterranean feeders, but no evidence exists. Little is known of the subterranean habits of the larvae, it is, however believed that the larval food is not provisioned by the adults, as larvae of *Pseudochodaeus* possess worn mandibles as well as well developed legs and claws (Carlson & Ritcher, 1974).

Ochodaeidae is divided into two subfamilies, the primitive Ochodaeinae and derived Chaetocanthinae (Scholtz, *et al.*, 1988). Ochodaeinae contains two tribes, Ochodaeini and Enodognathini, while Chaetocanthinae is divided into the primitive Pseudochodaeini, the intermediate Synochodaeini and the derived Chaetocanthini (Scholtz, *et. al.,* 1988).

There is disagreement among authors as to the exact position of this family in the Scarabaeoidea. There is, however, little doubt that the family is one of the more derived families within the "primitive" Scarabaeoidea lineage (Scholtz *et al.*, 1988; Scholtz, 1990). Carlson & Ritcher (1974) suggested that the Ochodaeidae and Hybosoridae are closely related, while Iablokoff-Khnzorian (1977) suggested relationship between Ochodaeidae and Aclopidae. Crowson (1981) implied, in a list of families of Scarabaeoidea, a relationship between Ochodaeidae, Hybosoridae and Geotrupidae, while Lawrence & Newton (1982),

Scholtz *et al.* (1988) and Browne (thesis: 1993) suggested relationship between Ochodaeidae, Hybosoridae and Ceratocanthidae.

Browne & Scholtz (1995) placed the Ochodaeidae in the geotrupid line of the passalid lineage. The geotrupid line consists of Geotrupidae and the ochodaeid group (containing Ochodaeidae and the hybosorid subgroups with Hybosoridae and Ceratocanthidae). Ochodaeidae is therefore the sistergroup of the hybosorid subgroup. This was reiterated by Browne & Scholtz (in press).

Ceratocanthidae

Members of the Ceratocanthidae (previously known as Acanthoceridae) are found in the forests of Australia, Asia, America and Africa as well as various islands, and are best represented in tropical areas. These beetles are small (2,5 - 7 mm) and are characterised by being able to roll up in a ball (Scholtz, 1990). Rolling into a ball is a defence adaptation (Crowson, 1981). All appendages can be retracted and the ventral surfaces of at least the head and thorax covered. The adults possess a large pronotum and short presternum and grooves to receive the retractable appendages. Adults as well as larvae stridulate (Crowson, 1981).

Both adults and larvae have been found in rotten wood and under bark and also in association with ants and termites. Specimens have also been collected in humus and it is thought that they might be fungus feeders (adult mouthpart structure supports the view that they are fungus feeders (Nel & Scholtz, 1990)).

The family consists of about 40 genera and more than 300 species (Scholtz, pers. comm.) and is considered to be one of the derived members among the more primitive Scarabaeoidea (Howden & Gill, 1988; d'Hotman & Scholtz, 1990b; Nel & Scholtz, 1990; Scholtz, 1990; Browne, thesis: 1993). Monophyly of the Ceratocanthidae is supported by the fact that all taxa in the family share two apomorphic wing articulation character states (Browne & Scholtz, 1995).

Ceratocanthidae is closely related to Ochodaeidae and Hybosoridae, Hybosoridae being the sistergroup (Howden & Gill, 1988; d'Hotman & Scholtz, 1990b; Nel & Scholtz, 1990; Scholtz,

1990; Browne, thesis: 1993). According to Browne & Scholtz (1995) Ceratocanthidae is part of the geotrupid line of the passalid lineage. The geotrupid line consists of the Geotrupidae and the ochodaeid group containing Ochodaeidae and the hybosorid subgroup.

Hybosoridae

Members of the Hybosoridae are widespread, with the main distribution in the tropics (Kuijten, 1978). There are about 28 genera with over 270 species. The size of the adults varies from small to moderate (5 - 15 mm). They are dark brown to black, smooth beetles and they are capable of deflexing their heads to conceal them beneath the pronotum. Larvae occur in decaying plant material, while adults are found in decaying animal material, usually in the early stages of the decay. Adults are also attracted to light and have been collected on flowers with a strong carrion smell.

Characters of the male genitalia, mouthparts and segmentation of the larval antennae and maxillary palpi support the division of the Hybosoridae into a primitive Old and a derived New World lineage (d'Hotman & Scholtz, 1990b; Nel & Scholtz, 1990; Scholtz, 1990; Browne, thesis: 1993). Hybosoridae have been placed between Trogidae and Ceratocanthidae, (Howden & Gill, 1988) but recently it was suggested that the family occupies a position between Ochodaeidae and Ceratocanthidae (d'Hotman & Scholtz, 1990b; Nel & Scholtz, 1990; Scholtz, 1990; Browne, thesis: 1993).

Hybosoridae is believed to be one of the derived members of the "primitive" Scarabaeoidea (Scholtz, 1990). Ceratocanthidae is at present considered the sistergroup of Hybosoridae (Howden & Gill, 1988; d'Hotman & Scholtz, 1990b; Nel & Scholtz, 1990; Scholtz, 1990; Browne, thesis: 1993; Browne & Scholtz, 1995; Browne & Scholtz, in press).

Scarabaeidae: Aphodiinae

Members of this subfamily are elongated, small (2 – 15 mm) with varying colours (brown, black or grey). The elytra are with or without markings, and the pronotum is with or without sculpturing. Aphodiinae is a large cosmopolitan group, consisting of approximately 1200 species (Nel & Scholtz, 1990). These beetles are predominantly a cool-climate taxon, in warmer parts of the world the Aphodiinae are restricted to humid forest areas (Crowson, 1981). They are usually referred to as dung beetles, but not all members feed on faeces,

some are detritivores feeding on organic material in the soil or on fungi (Ritcher, 1966; Ratcliffe, 1988). In hot, dry savannah areas of Africa, India and Australia the rapid and complete drying out of exposed dung largely prevents its utilisation by Aphodiinae. The larvae are similar to those of the Scarabaeinae, but lack a hump. Larvae are either dung feeders or feed on organic matter found in the soil. A number of genera are termitophilous and in Britain the species *Aphodius porcus* is known to parasitise the nests of some *Geotrupes* species (Halffter & Matthews, 1966). Adults do not "provision" the larvae as is found in the Scarabaeinae. In many cases the eggs are deposited deep in the dung mass and larvae mature before the mass becomes uninhabitable through desiccation (Howden, 1955).

Depending on the author, the group may be treated as a subfamily of the Scarabaeidae, as well as a separate family. There is disagreement as to how many tribes (or subfamilies if the taxon is treated as family) comprise the subfamily. Schmidt (1922) listed five subfamilies, Tangeleder & Krikken (1982) listed seven, while d'Hotman & Scholtz (1990a) listed three subfamilies, Aphodiinae, Eupariinae and Psammodiinae. Scholtz (1990) treated the subfamilies suggested by d'Hotman & Scholtz (1990a) as tribes and added Aegialiini. Aegialiini was previously treated as a subfamily and many workers believed Aphodiinae and "Aegialiinae" to be closely related (Stebnicka, 1985; Cambefort; 1987; Nel & Scholtz, 1990; d'Hotman & Scholtz, 1990a).

The subfamily is treated as one of the more primitive members of the derived Scarabaeoidea (d'Hotman & Scholtz, 1990a; Scholtz, 1990; Browne, 1993). Browne (thesis: 1993) suggested that the taxon is closely related to Aulonocneminae, and secondarily to Scarabaeinae. Browne & Scholtz (1995) placed Aphodiinae in the scarabaeid lineage (the scarabaeid lineage contains those taxa traditionally included in the Scarabaeidae: Aegialiinae, Aulonocneminae, Aphodiinae, Scarabaeinae, Orphninae, Melolonthinae, *Acoma*, Chasmatopterinae, Hopliinae, Oncerinae, Rutelinae, Dynastinae, Trichiinae, Cetoniinae and Valginae).

Scarabaeidae: Scarabaeinae

Members of the Scarabaeinae, also known as true dung beetles are small to large (1 - 50 mm), brown, black or even sometimes blue, green or purple beetles. The subfamily

Scarabaeinae is a large, cosmopolitan group, with most adults as well as larvae feeding on dung (coprophages). There are, however, also carrion (necrophagy), fungus (e.g. wild mushrooms) and litter feeders amongst the Scarabaeinae. They can be classified ecologically by the way they treat the dung. Members of the Scarabaeinae either feed on the dung where it falls or the males and females excavate tunnels and chambers which they provision with dung and in which the females then lay eggs and care for the larvae. Taking pieces of dung into the hole also removes it from areas accessible to flies - an important ecological factor. Scarabaeinae which breed inside the dung pad without burying it are known as endocoprids. Nests of paracoprid Scarabaeinae are always connected to the food supply either directly or by means of a tunnel. Telecoprid species form dung balls and roll them backwards, burying them in a chamber in the soil. In southern Africa, members of the Scarabaeinae occur in all terrestrial vegetation and habit types, from deserts to tropical areas. Activity varies from diurnal, nocturnal to crepuscular.

The adults provide brood chambers and may remain with the brood, caring for it (Halffter & Edmonds, 1982). The larvae have a characteristic hump in the middle of the dorsal surface.

The subfamily is divided into twelve tribes, with many subtribes (Hanski & Cambefort, 1991). Scarabaeinae occupy an intermediate position between Aphodiinae and Melolonthinae (Howden, 1988; Scholtz, 1990) and there is little doubt that it is one of the more primitive members of the derived Scarabaeoidea.

Browne & Scholtz (1995) placed the Scarabaeinae in the scarabaeid lineage together with the other subfamilies of the Scarabaeidae.

Scarabaeidae: Melolonthinae

Members of this cosmopolitan subfamily (adults known as leaf chafers and larvae as white grubs) are diverse, with most adults crepsucular or nocturnal. Members of the Melolonthinae and night-flying Rutelinae (there are also brightly coloured day-flying rutelids - discussed in the following section) sometimes look very similar. The most reliable character to use in distinguishing between the two groups, is that the tarsal claws of the Melolonthinae are equal and immovable, while the Rutelinae possess a movable tarsal claw (at least on the hind legs, which are of unequal size). The feeding habits of the adults vary from non-feeding to feeding

on either flowers or green foliage. Larvae (typically scarabaeoid in appearance) feed on roots, humus or rarely, on dung (Scholtz, 1988; Lawrence & Britton, 1991).

The tribes constituting Melolonthinae are ill-defined and polyphyletic (Ritcher, 1967; Scholtz, 1990). There is, however, little doubt that this taxon is one of the more derived members of Scarabaeoidea (Yadav & Pillai, 1976; Howden, 1988; d'Hotman & Scholtz, 1990ab; Nel & Scholtz, 1990; Scholtz, 1990; Browne, thesis: 1993). Presently it is considered as a sistergroup of Rutelinae or Rutelinae-Dynastinae (Ritcher 1969a; Meinecke, 1975; Yadav & Pillai, 1976; Caveney, 1986; Scholtz 1990; Lawrence & Britton, 1991).

Browne (1993) indicated, on the basis of wing articulation characters that the subfamily is the sistergroup of Rutelinae + Dynastinae + Cetoniinae + Trichiinae + Valginae. He also suggested, because of shared synapomorphic character states, that *Acoma*, Hopliinae, Oncerinae and Chasmatopterinae should be included in the subfamily Melolonthinae.

Browne & Scholtz (1995) placed Melolonthinae in the scarabaeid lineage, together with groups traditionally included in the Scarabaeidae.

Scarabaeidae: Rutelinae

Members of this subfamily are diverse and cosmopolitan and also known as leaf chafers (adults) and white grubs (larvae). Adults vary from 4 - 15 mm. Adults are foliage feeders (and either dull brown or grey night-flying or brightly coloured day fliers) while the larvae feed on plant roots as well as decaying plant matter (Scholtz, 1990). Many species of*Anomala* feed little or not at all (Ritcher, 1958). Larvae are typically scarabaeoid in appearance. Females tunnel into soil or litter to lay eggs. Eggs have been found up to one metre under the ground.

Rutelinae is a well-defined subfamily consisting of many ill-defined tribes, (Browne, thesis: 1993), but are members of the derived Scarabaeoidea (Howden, 1982; Scholtz, 1990). According to various authors (Ritcher, 1969a; Howden, 1982; d'Hotman & Scholtz, 1990a, Nel & Scholtz, 1990; Scholtz, 1990) Rutelinae are closely related to Melolonthinae as well as Dynastinae. Meinecke (1975), Howden (1982) and Browne (thesis: 1993) considered Rutelinae as more closely related to members of the Dynastinae, with Melolonthinae a

sistergroup to both these taxa.

Browne & Scholtz (1995) placed Rutelinae in the scarabaeid lineage together with the other members of the family Scarabaeidae.

Scarabaeidae: Hopliinae

Members of this subfamily have a wide distribution, found in the Nearctic, Palaearctic, Neotropical, Oriental and Afrotropical regions (Hardy, 1977). Most adults are active in the daytime and feed on flowers (their mouthparts being developed for pollen feeding) but there are also some instances where they are known to feed on leaves and fruit (the mouthparts of species feeding on leaf material have been adapted and some parts have become toothed and sclerotised) (Nel & Scholtz, 1990). Members of the Hopliinae are small, usually brightly coloured, hairy beetles. They have extraordinarily developed hind legs and claws which are used for anchoring themselves to the composite flowers that they feed on. The larvae develop in the ground and are saprophagous or rhizophagous (Iablokoff-Khnzorian, 1977).

Hopliinae contains two tribes, Hopliini and Pachycnemini (d'Hotman & Scholtz, 1990a,b). This subfamily has been put into different groups over the years. Leng (1920) grouped it together with the Oncerinae, and it is sometimes also incorporated into the Rutelinae (Scholtz & Holm, 1985), or the Melolonthinae (Hardy 1977). Browne (thesis: 1993) found that, according the wing articulation characters, the taxon be placed as a tribe under the Melolonthinae.

Browne & Scholtz (1995) placed Hopliinae in the scarabaeid lineage together with the rest of the members of the Scarabaeidae.

Scarabaeidae: Dynastinae

Members of this family, also known as the rhinoceros beetles are elongated, round, black or brown beetles varying from 10 - 45 mm. The males of many species possess large horns on the head or thorax. The mouthpart structure of the adults indicates that they are mostly sap-feeders or even perhaps fungi-feeding (Nel & Scholtz, 1990). Adults feed on parts of plants below the ground-like stems, shoots or tap roots (Ritcher, 1958). Adults are nocturnal and attracted to light. Most dynastines have an annual life-cycle but some larger Australian

species require two or even three years for their development (Carne, 1957). Larvae are typically scarabaeoid and are known to feed either on dung, roots of plants, humus or other organic matter.

Dynastinae is a well-defined subfamily consisting of many tribes. The subfamily is also a member of the more derived Scarabaeoidea (Scholtz, 1990). The taxon is thought to be closely related to Rutelinae on the basis of many different morphological characters like the presence of unequal tarsal claws, abdominal spiracle patterns, mouthparts, male genitalia and wing articulation characters (Ritcher, 1969a; Howden, 1982; Nel & Scholtz, 1990; Scholtz, 1990; Browne, thesis: 1993).

Browne & Scholtz (1995) placed the Dynastinae in the scarabaeid lineage together with other members of the Scarabaeidae.

Scarabaeidae: Cetoniinae

The Cetoniinae, also known as fruit and flower chafers is a large cosmopolitan subfamily, with approximately 500 genera. The adults are usually brightly coloured, stout beetles varying between 10 - 70 mm. Adults are mostly flower and foliage feeders (feeding on plant juices like sap or juices of ripening or overripe fruit (Ritcher, 1958)) or predatory in the nests of social Hymenoptera. Some species are also common on flowers where they feed on pollen and nectar. Most members of Cetoniinae are diurnal in habit and some gather in trees.

Larvae are typically scarabaeoid in appearance and feed on decomposing vegetable matter, but some have been found in ant or bird nests (Scholtz, 1990).

The Cetoniinae consists of many tribes. Cremastocheilini are perhaps the most primitive, feeding in termite nests. Adults of the tribes Goliathini and Gymnetini feedmainly on pollen and sap; members of Cetoniini feed on fruit, gum and flowers, suggesting them to be very specialised; while members of the Diplognathini are attracted to rotten fruit (Nel & Scholtz, 1990).

Leng (1920) placed the taxon under Rutelinae, but the Cetoniinae is now considered as the

sistergroup of Rutelinae and/or Dynastinae (Ritcher, 1969a; Meinecke, 1975; Howden, 1982; Caveney, 1986; d'Hotman & Scholtz, 1990a; Nel & Scholtz, 1990; Scholtz, 1990; Browne, thesis: 1993). Trichiines and valgines are considered the primitive sistergroup of Cetoniinae (Browne, thesis: 1993), while Rutelinae and/or Dynastinae are the primitive sistergroup of trichiines, valgines (Scholtz (1990) referred to the trichiines and valgines as tribes under Cetoniinae; in this thesis they will be referred to as subfamilies) and cetoniines (Krikken, 1984). Browne (thesis: 1993) believes that Trichiini, Valgini and Cetoniinae are very closely related, but suggests that Trichiini is more correctly placed as a tribe under Cetoniinae.

Browne & Scholtz (1995) placed Cetoniinae in the scarabaeoid lineage which contains the taxa traditionally included in the Scarabaeidae.

Scarabaeidae: Trichiinae

This is a cosmopolitan group of insects. Adults either feed on pollen, sap flowing from bark (Nel & Scholtz, 1990) or flowers (Howden, 1968; Crowson, 1981). Trichiines are strong fliers. Mimicry of Aculeate Hymenoptera by members of *Trichius* and *Apeltastes* species, takes place (Howden, 1968; Crowson, 1981). Larvae (described as looking like larvae of Cetoniinae by Delgado-Castillo & Moron, 1991) feed on decaying wood (Ritcher, 1966).

The taxon has been regarded as a subfamily (Blackwelder, 1944; Howden, 1968; Krikken, 1984) as well as a poorly defined tribe under Cetoniinae (Leng, 1920; Ritcher, 1969; Caveney, 1986; Scholtz, 1990; Browne, 1993).

The genus *Osmoderma* also poses a ranking problem. Browne (thesis: 1993) suggested that, on the basis of wing articulation characters, the genus *Osmoderma* be elevated to a subfamily and that Trichiini be grouped under a primitive tribe of Cetoniinae.

Browne & Scholtz (1995) placed this group in the scarabaeoid lineage as a subfamily, together with the taxa grouped in the Scarabaeidae (in this thesis the taxon is referred to as a subfamily of the Scarabaeidae).

Scarabaeidae: Valginae

This taxon consists of about 265 species in 31 genera world wide, occurring in all the major zoogeographical regions, except the Neotropics (Krikken, 1978). Adults are associated with flowers and feed on nectar and pollen, while others (species belonging to *Microvalgus*) have been associated with termites. In for example North America all stages of the genus *Valgus* have been encountered beneath bark at the bases of trees and in association with termites (Ritcher, 1966). Mouthparts of the valgines suggest that they feed on pollen or nectar, and that their mandibles are the same as that of other pollen feeders like Cetoniinae and some Hopliinae (Nel & Scholtz, 1990).

Valginae is a well-defined subfamily whose monophyly is supported by several derived characters (Browne, thesis: 1993) and is a member of the more derived Scarabaeoidea (Krikken, 1978; d'Hotman & Scholtz, 1990a; Nel & Scholtz, 1990). Scholtz (1990) placed the taxon as a tribe of the Cetoniinae while d'Hotman & Scholtz (1990a) consider Valginae to be the most derived scarab subfamily. Krikken (1984) considered the valgines to be the sistergroup of trichiines and together the sistergroup of Cetoniinae.

Browne & Scholtz (1995) included the valgines in the scarabaeid lineage as a subfamily of Scarabaeidae (in this thesis the taxon will also be referred to as a subfamily).

Scarabaeidae: Oncerinae

Oncerinae is a small subfamily, occurring in California (Saylor, 1938).

This subfamily is poorly defined but closely related to Melolonthinae (Leng, 1920; Saylor, 1938). Oncerinae is regarded as a separate subfamily on the basis of the position of the abdominal spiracles. It is placed in the derived scarabaeoid lineage (d'Hotman & Scholtz, 1990b; Browne, thesis: 1993).

Browne & Scholtz (1995) placed the oncerines as a subfamily in the scarabaeid lineage.

Scarabaeidae: Chasmatopterinae

This group is considered by Scholtz (1990) as of uncertain phylogenetic status. It is a poorly

defined subfamily, but closely related to Melolonthinae (d'Hotman & Scholtz, 1990b), being removed from the melolonthines on the basis of the position of the adult abdominal spiracles (7^{th} and 8^{th} segments spiracles situated on the pleural membrane) (Saylor, 1938). Ritcher (1969a), however, found that the spiracles are actually situated in the lower parts of the tergites.

After investigation of the wing articulation characters, Browne (thesis: 1993) suggested that this taxon be placed as a genus under the subfamily Melolonthinae. Browne & Scholtz (1995) included members of this taxon as a subfamily in the scarabaeid lineage together with other subfamilies constituting the Scarabaeidae.

Scarabaeidae: Orphninae

Orphninae are a small Old World group consisting of a few genera, mostly in the genera *Orphnus* and *Hybalus* (Nel & Scholtz, 1990). Adults as well as larvae have been recorded feeding on potatoes and sugar cane (Paulian & Lumaret, 1982).

Paulian & Lumaret (1982) suggests that there is enough evidence that the taxon be placed as a family (closely related to the Melolonthinae). Browne (thesis: 1993), because of wing articulation characters, proposed that this group is the sistergroup of Melolonthinae, Rutelinae, Dynastinae, Trichiinae, Cetoniinae and Valginae. Browne & Scholtz (1995) placed the Orphninae in the scarabaeid lineage together with the rest of the subfamilies constituting the Scarabaeidae.

3. EVALUATION OF ORGAN SYSTEM CHARACTERS OF THE SCARABAEOIDEA

Introduction

The monophyly of the Scarabaeoidea is an undisputed fact (Lawrence and Britton, 1991). Over the years, however, there has been considerable speculation about the nature of the Scarabaeoidea ancestor or the most primitive extant scarabaeoid, as well as different opinions on the nature of the outgroup or sistergroup of the superfamily.

Authors speculating on which of the present Scarabaeoidea taxa is the most primitive member of the superfamily, include Crowson (1955), Iablokoff-Khnzorian (1977), Howden (1982) and Scholtz *et al.* (1987). Crowson (1955) proposed that the ancestors were small, convex beetles that burrowed in soil and that they most probably fed on fungi. According to Crowson, Lucanidae and then Trogidae are the most primitive living members of the superfamily. Iablokoff-Khnzorian (1977) proposed that the ancestor was something like a modern-day pleocomid and that it occurred in rotting wood. He believed that Passalidae is the most primitive scarabaeoid. Howden (1982) believed that Passalidae and Lucanidae were the most primitive scarabaeoids; he made this suggestion based on a partial phylogenetic analysis of the superfamily. Paulian (1988) also believed that Passalidae and Lucanidae were the most primitive members of the superfamily. *Glaresis* (previously placed under Trogidae, but elevated to family level by Scholtz *et al.* (1987)) is presently believed to be the most primitive living scarabaeoid and that it lies close to the basic evolutionary stock from which the Scarabaeoidea evolved Browne & Scholtz (1995).

Another point of dispute was the outgroup of the Scarabaeoidea. Groups within the Polyphaga favoured as possible outgroups include the Dascilloidea, a member of the Heterogastra as well as the Haplogastra (Hydrophiloidea, Staphylinoidea, Histeroidea and Scarabaeoidea). (As mentioned in Chapter 1, Jeannel & Paulian (1944) suggested that the Polyphaga be divided into Haplogastra and Heterogastra - this system is, however, not presently favoured as it is difficult to substantiate the relationship between the superfamilies based on larval characters).

Crowson (1981) as well as Scholtz (1990) favoured the Dascilloidea (Heterogastra) as an outgroup of the superfamily. Members of the Dascilloidea have close resemblance to Scarabaeoidea. Resemblance includes similarity between larval Dascilloidea and larval Scarabaeoidea (Lawrence, 1991); meso-thoracic spiracles in the adults (Ritcher, 1969b); the similarity between the median lobe of the aedeagus of the adult Dascilloidea and groups in the Scarabaeoidea like *Pleocoma* and *Diphyllostoma* (d'Hotman & Scholtz, 1990); similarity between the exocone ommatidium structure of Dascilloidea and that of Passalidae (Caveney, 1986); similarity of the trilobe male genitalia of Dascilloidea and some primitive Scarabaeoidea like Glaresidae (d'Hotman & Scholtz, 1990); and the similarity between the mouthparts of the two groups (Nel & Scholtz, 1990).

There are, however, authors like Lawrence & Newton (1982) and Lawrence & Britton (1991) who do not agree with the assumption that Dascilloidea is the outgroup of the Scarabaeoidea. They believe that the similarities in the larvae of the two groups are associated with larvae found in soil, and that these characters are therefore primitive (plesiomorphic characters do not indicate relationship in cladistics). Kukalová-Peck & Lawrence (1993), who studied the hindwing in Coleoptera, also do not agree with the relationship between Dascilloidea and Scarabaeoidea, but support the idea that there is a strong relationship between Haplogastra and Scarabaeoidea.

Scholtz *et al.* (1994) completed a comprehensive cladistic analysis of the Scarabaeoidea families, based on numerous morphological characters and re-assessed characters from previous studies. Characters studied and re-assessed by Scholtz *et al.* (1994) included: antennae, canthus of the eye, ommatidium structure, mandibles, maxillae, labium, tentorium, epipharynx, legs, trochantin, procoxae, mesocoxae, mesothoracal spiracles, hindwing venetation, hindwing articulation, wing base, abdominal spiracles, male genitalia, ovarioles and karyotype. In all 87 adult and 44 larval character states were assesses and a general groundplan for the above mentioned characters was established. The analysis of the above-mentioned characters provided evidence that members of Glaresidae are the most primitive living scarabaeoids and therefore the probable sistergroup of the Scarabaeoidea.

A complete phylogeny of the superfamily was, however, not available up to 1995, and this despite the fact that a large database of characters was previously established

(Scarabaeoidea is morphologically one of the best-studied beetle groups. There have been numerous broadly-based comparative studies covering most major structures.). Howden in 1982 attempted a partial phylogeny, but many available characters and several taxa were not included, and the data matrix was not subjected to a computer-based cladistic analysis. Browne & Scholtz (1995) used hindwing articulation and hindwing base characters (two of the groups of characters also utilised by Scholtz *et al.* (1994) when they determined that Glaresidae was the most primitive living scarabaeoid and the sistergroup of the superfamily) to reconstruct the phylogeny of the Scarabaeoidea. According to the authors, the choice to "ignore" the rest of the characters (used by Scholtz *et al.*, 1994) to reconstruct intermediate and higher taxonomic levels within the Scarabaeoidea, was because they are too conservative or too homoplastic.

Browne & Scholtz (1995) constructed a cladogram of thirteen scarabaeoid taxa and seventy-three single- and multistate wing characters, which are 107 steps long and with a consistency index of 0.850. Although the study examined all 13 families, using for the first time taxa identified by Scholtz (1990) as being of uncertain phylogenetic status, it was very limited in that the resulting phylogram was based on only three character complexes. The authors, however, suggested that wing related characters are the most reliable of all structures in determining relationships among higher scarabaeoid taxa.

Previously, taxa within the superfamily were divided into primitive, intermediate and derived groups (Scholtz, 1990 and Browne, thesis: 1993). Browne & Scholtz (1995), however, replaced group names by a hierarchical system naming the components of the phylogenetic tree: lineage, line, group, subgroup and infragroup. Where more than one terminal taxon was present, Browne & Scholtz (1995) named the most primitive included taxon. The phylogenetic analysis of Browne & Scholtz indicated that there are two basal lineages, one with Glaresidae and the other with passalid-scarabaeid lineage, where the glaresid lineage is the sistergroup of the passalid-scarabaeid lineage. The passalid lineage (Passalidae, Lucanidae, Diphyllostomatidae, Glaphyridae, Trogidae, Bolboceratidae and Pleocomidae) comprises two lines, the passalid line and the geotrupid line. The passalid line consists of Passalidae and the lucanid group (Lucanidae and Diphyllostomatidae) and the glaphyrid group (Glaphyridae, Trogidae, Bolboceratidae and Pleocomidae). The glaphyrid group consists of Glaphyridae and the trogid subgroup (Trogidae, Bolboceratidae and

Pleocomidae). The trogid subgroup can be further divided into Trogidae and the bolboceratid infragroup (Bolboceratidae and Pleocomidae). The geotrupid line consists of Geotrupidae and the ochodaeid group (Ochodaeidae, Hybosoridae and Ceratocanthidae). The ochodaeid group consists of Ochodaeidae and the hybosorid subgroup (Hybosoridae and Ceratocanthidae). The scarabaeid lineage contains all the taxa traditionally included in the Scarabaeidae, namely Aegialiinae, Aulonocneminae, Aphodiinae, Scarabaeinae, Orphninae, Melolonthinae, *Acoma,* Chasmatopterinae, Hopliinae, Oncerinae, Rutelinae, Dynastinae, Cetoniinae, Trichiinae and Valginae.

Recently, Browne & Scholtz (in press) brought together all available data (including all adult and larval characters considered by Scholtz *et al.* (1994) – mentioned earlier) and proposed a phylogenetic analysis of all adult and larval characters from the thirteen currently recognised families of the Scarabaeoidea.

One of the aims of this thesis is to use characters from the different organ systems of representative members of the superfamily to determine whether the evolution of these characters agrees with or refutes previous phylogenetic assumptions (discussed in the introduction of this chapter). Since no groundplan for the organ systems is available and one is needed to construct a cladogram (and eventually to reconstruct the phylogeny of the superfamily) from the organ systems, one was constructed. Character transformations were decided upon by studying literature pertaining to general internal insect morphology, even covering groups like Collembola, in order to obtain a clear picture of the general trends in Insecta. The fact that Glaresidae is regarded as the most primitive living scarabaeoid and the sistergroup of the superfamily was also taken into account. From this information, a hypothetical groundplan for each of the organ systems was constructed.

The aims of this chapter are to:

- Discuss character evaluation and character state transformations of the organ systems.
- Discuss the available literature on the different organ systems.
- Construct a hypothetical groundplan for each of the organ systems.

Character evaluation and character state transformations

Cladistic methods were implemented to analyse the morphological characters of the organ

systems of the Scarabaeoidea. Hennig's classical perspective on evaluating characters is followed whereby a series of logical deductions based on phylogenetic definitions of apomorphous and plesiomorphous homologies are made. These cladistical methods are described in Wiley (1981) and will be discussed in context of the morphological characters used in this thesis in the following section.

All analyses were based on the assumption that all morphological structures studied, for example the ganglia, are homologous. How the evaluation of characters was done is explained in the following paragraphs:

The most primitive state is 0 and increasingly derived character states are given sequentially higher numbers. The number of steps from one state to another is specified as the difference between their state numbers. Therefore a change from 0 to 1 is specified as one step, from 0 to 8 as eight steps etc. The list of symbols, therefore, represents a linear transformation series and it is assumed that to get from state 0 to state 3 the character must proceed progressively through states 1 and 2.

A single morphological character e.g. the number of visible thoracic ganglia was divided into different character states. Three different character states of this morphological character are present in adult Scarabaeoidea. They are:

1. all three ganglia visible;
2. meso- and metathoracic ganglia united;
3. pro-, meso- and metathoracic ganglia united.

These states form a transformation series, but this series must be polarised (the plesio- and apomorphic states must be decided upon). This is done by implementing Hennig's outgroup rule: "given two characters that are homologues and found within a single monophyletic group, the character that is also found in the sistergroup is the plesiomorphic character whereas the character found only within the monophyletic group is the apomorphic character" (Wiley, 1981). This process of hypothesising which of the character states in the transformation series are apomorphic, is known as Hennig's augmentation scheme.

The polarised transformation series is then coded (allotted numerical values) from 0

(plesiomorphic) to 1 to 2 etc. representing intermediate and derived states.

The different character states of the number of thoracic ganglia visible for example, that are ordered and polarised can be depicted as follows:
0 (plesiomorphic state) - all three ganglia visible;
1 (intermediate apomorphic state) - meso- and metathoracic ganglia united;
2 (derived apomorphic state) - pro- meso and metathoracic ganglia united.

All of the character states of the morphological characters (internal organs and ovipositor) of the Scarabaeoidea form an ordered, linear transformation series. In some instances, e.g. no males were collected from a specific family, and treated as missing data. Missing data were then coded as ? in the character matrix.

The character states were assembled into a character matrix, and that used in the cladistic analysis. The complete data matrix contains all character states of each character coded. The data matrix were subjected to PAUP (Swofford, 1985) on an Apple Macintosh. Minimization of the number of character state changes were used to optimize the phylogram. Trees were produced by the branch-and-bound algorithm, Farris optimization and outgroup rooting.

Structure of the alimentary canal in insects

In its simplest form, the alimentary canal of insects consists of a tube consisting of three distinct areas. They are the ectodermal stomodeum (foregut) with a fine chitinous lining, the endodermal mesenteron (midgut) without the chitinous lining and the ectodermal proctodaeum (hindgut), again with a chitinous lining (Snodgrass, 1935; Crowson, 1981; Romoser, 1981). These three areas are separated from one another by the cardiac and pyloric valve respectively. The various regions of the alimentary canal are modified anatomically or physiologically to perform various functions. The three primary regions of the alimentary canal of Coleoptera are also differentiated into the foregut, midgut and hindgut. The oesophagus and midgut of members of the non-feeding Coleoptera are very thin-walled and slender, and the midgut lacks an opening into the hindgut. The hindgut is also short and not differentiated into different areas. In feeding beetles the alimentary canal is considerably longer than the body and the mid- as well as the hindgut are thrown into loops and folds.

Members of the Oedemeridae that feed on pollen and nectar have a notably shorted alimentary canal (Crowson, 1981).

FOREGUT

The main function of the foregut is storage of food, sometimes, however, it helps to fragment the food before it passes to the midgut. The most primitive form of the stomodeum (foregut) is little more than an inlet for food to the midgut and appears as a tube that is not differentiated into any regions (Collembola) (Snodgrass, 1935; Romoser, 1981). A more derived form of the foregut is a long tube usually with the middle part enlarged to form an additional storage chamber. Five primary regions can be distinguished: the buccal cavity, pharynx, oesophagus, crop and proventriculus (Orthoptera, Odonata, Lepidoptera, Diptera and some members of the Coleoptera). A very slender oesophagus without distinct areas, is present in many Staphylinoidea that practise extra-oral digestion (Crowson, 1981). Extra-oral digestion also occurs in Hydrophiloidea, Staphylinidae and Histeridae (which are proposed outgroups for the Scarabaeoidea). The foregut of Dascilloidea (also one of the proposed outgroups of the Scarabaeoidea) consists of a short and narrow muscular pharynx, a broader short oesophagus and a large crop (Kasap & Crowson, 1975). The crop is an enlargement of the foregut in which food is stored. Usually it represents the posterior area of the oesophagus, but in some fluid feeders it is a lateral diverticulum. A short, narrow, thick walled proventriculus is sometimes present. In fluid feeders the proventriculus is absent except for a simple valve at the origin of the midgut. A valve is also present (between the fore- and midgut) in many other insects, and often circular muscles form a sphincter at the entrance of the midgut.

MIDGUT

The midgut is separated from the foregut by the cardiac or stomodeal valve. It is also called the ventriculus and is without differentiation and serves as the insect's stomach (Romoser, 1981). An undifferentiated ventriculus is present in the more primitive insects such as Plecoptera and Orthoptera. In the Hemiptera, the midgut is differentiated into three distinct areas. Gastric caecae or blind pouches may occur at the posterior end which surround the pyloric valve that separates the midgut from the hindgut (Treherne, 1967). In many Coleoptera the ventriculus is covered with small papillae. These structures are crypts rather than true caecae (Wigglesworth, 1972). The function of caecae is to provide a safe place for alimentary canal bacteria (Glasgow, 1914). Coleoptera herbivores tend to possess a long convoluted midgut whereas pollen or nectar feeding beetles as well as carnivores,

possess a notably shorter midgut (Crowson, 1981). The midgut of Dascilloidea consists of a short ventriculus (Kasap & Crowson, 1975), whereas members of the Histeridae possess a long, narrow midgut with an almost constant diameter. Long, evenly distributed papillae over its entire length are present (Crowson, 1974).

HINDGUT

The hindgut is the most posterior region of the alimentary canal. In its primitive form it is a simple tube constituting only a passway from the midgut to the anus. In its more derived form the anterior margin is marked by the pyloric valve, and just posterior of this valve, the appearance of the bases of the Malpighian tubules. The Malpighian tubules are typically long, slender and convoluted. The number of Malpighian tubules varies from four (found in Lepismatidae) six in other Apterygota, 50 to 60 in Odonata and Plecoptera, six to eight in Neuroptera, and four to six in Coleoptera (the most common number is four) (Snodgrass, 1935). Six Malpighian tubules are present in the Dascilloidea and the hindgut is differentiated into different areas (Kasap & Crowson, 1975). The Histeroidea possess 6 Malpighian tubules inserted at the beginning of the hindgut; the hindgut is relatively short possessing 6 longitudinal thickenings immediately before the junction with the rectum. The rectum is a muscular structure (Crowson, 1974).

The hindgut is further subdivided into the anterior intestine and posterior intestine that are separated internally by the rectal valve. The anterior region is often subdivided into the anterior ileum and posterior colon. Adjoining the colon is the rectum ending in the anus (Snodgrass, 1935; Romoser, 1981).

Morphological characters of the alimentary canal of the Scarabaeoidea, and phylogenetic interpretations

FOREGUT

In the Scarabaeoidea the foregut is relatively simple and in the primitive groups only differentiated into two areas, the pharynx and oesophagus, e.g. Passalidae and Scarabaeinae (Lewis, 1926; Becton, 1930; Patterson, 1937). In the more derived groups such as the Melolonthinae, Rutelinae and Cetoniinae no distinction can be made between these two areas (personal observation). The foregut and midgut are always separated by the oesophageal valve (Lewis, 1926; Fletcher 1930; Swingle, 1930; Patterson 1937; Cheung & Low, 1975). In some derived groups a lateral, sac-like diverticulum is present, forming the

crop (personal observation).

MIDGUT

The midgut of the primitive, as well as some of the more derived Scarabaeoidea, is usually differentiated into an anterior and posterior region, but in groups like Scarabaeinae, Melolonthinae and Cetoniinae no differentiation is present (Becton, 1930; Fletcher, 1930; Berberet & Helms, 1972; Cheung & Low, 1975).

Small to larger papillae (caecae) are present on the midgut of species belonging to the Passalidae and Cetoniinae (Patterson, 1937; Cheung & Low, 1975).

HINDGUT

Four Malpighian tubules occur throughout the Scarabaeoidea (Lewis, 1926; Swingle, 1930; Lison, 1938; Crowson, 1981). In primitive groups like the Passalidae (Patterson, 1937) the tubes are arranged in two pairs that are connected on each lateral area of the hindgut but in the more derived groups, for example the Melolonthinae (Lison, 1938), the position of attachment is shifted - two of the tubes open dorsally into the same opening while the other two open one on each side of the hindgut. The Malpighian tubules of some of the more primitive groups are of uniform length and without any protuberances (such as in the Passalidae (Patterson, 1937)). In the more derived groups for example Melolonthinae (Lison, 1938), the two dorsal tubes are shorter than the other two that open laterally. All four tubes possess protuberances covering them.

There is a clear distinction between the hindgut of the primitive Scarabaeoidea and that of the more derived groups. The hindgut of the more primitive Scarabaeoidea e.g. the Passalidae (Lewis, 1926; Patterson, 1937) is divided into a short proximal ileum, longer distal ileum, slender colon, short but enlarged rectum and anus.

In the more derived groups belonging to the Scarabaeoidea, e.g. in the Scarabaeinae (Becton, 1930) and in the Melolonthinae (Lison, 1938) no distinction can be made between the anterior ileum and posterior colon. The hindgut is divided into the ileum, rectum and anus.

PHYLOGENETIC INTERPRETATION

Character 1: Structure and regions of foregut:

0 - pharynx and oesophagus distinguishable;

1 - foregut a simple tube, not externally divided into different areas;

2 - crop is present in the form of a lateral sac-like diverticulum

Character 2: Length of midgut:

0 - midgut short;

1 - midgut very long and convoluted

Character 3: Regions of midgut:

0 - midgut divided into anterior and posterior regions;

1 - midgut not differentiated into different areas, one long tube

Character 4: Attachment of the Malpighian tubules:

0 - two paired Malpighian tubules attached laterally;

1 - two of the tubes open dorsally at same position while other two still open one on each side of hindgut

Character 5: Different areas of hindgut:

0 - five regions of hindgut present, proximal ileum, distal ileum, colon, rectum and anus;

1 - three regions of the hindgut present - ileum, rectum and anus

Structure of the central nervous system in insects

The central nervous system of insects consists of a group of ganglia connected to each other by connectives (Romoser, 1981). In many embryonic insects there is a paired ganglion in each segment of the body, but these show some degree of fusion before the insect emerges from the egg. The most anterior ganglion, (the brain or cerebral ganglion) is situated in the head, lying above the anterior end of the foregut. It is followed by the ventral nerve cord with the second ganglion, the suboesophageal ganglion (Matsuda, 1965; Huber, 1974). The three thoracic segments each possess a ganglion and the abdomen possesses mostly eight definite segmental ganglia corresponding to the first eight abdominal somites. Eight abdominal ganglia are also the largest number of ganglia occurring in larval and adult insects. Eight abdominal ganglia are typically found in members of the Thysanura. The last abdominal ganglion is always compound, and derived from the ganglia of the last four abdominal segments.

The ganglia of the abdomen, however, are usually subject to displacement anteriorly so that the ganglion of a particular segment may occur in another segment (Crowson, 1981). All the ganglia in the central nervous system have a tendency to unite with one another, for example Diptera, Hymenoptera and some Coleoptera (Romoser, 1981). All the ventral ganglia in members of *Musca* (Diptera) are fused together into one large ganglionic mass (Chapman, 1969).

In the Coleoptera the ancestral number of discrete abdominal ganglia is six with the first one more or less fused to the ganglion in the metathorax (Crowson, 1981; Romoser, 1981). The other ganglia are connected to each other by clearly distinguishable connectives.

Morphological characters of the central nervous system of Scarabaeoidea, and phylogenetic interpretations

The nervous system of the Scarabaeoidea consists of the suboesophageal ganglion, pro-, meso-, and metathoracic ganglia and the six abdominal ganglia.

The different ganglia are united to each other with connectives that may vary in length. The connectives, especially those that connect the abdominal ganglia are prominent and long in the more primitive taxa of the Scarabaeoidea, for example Passalidae and Lucanidae. These abdominal ganglia can stretch posteriorly in the abdomen as far back as the beginning of the hindgut. However, in the more derived taxa, the connectives tend to shorten, bringing the ganglia closer together. The ganglia are therefore moved more anteriorly because of the shortening of connectives. The connectives can shorten so much that the different ganglia tend to fuse to one another. This situation is present in the more derived groups for example Melolonthinae (Menees, 1961; Berberet & Helms, 1972). The abdominal ganglia are then situated more or less on top of the metendosternite. Not only the connectives between the abdominal ganglia shorten, but also those between the thoracic ganglia. These ganglia then move towards the abdominal ganglia to form a ganglionic mass consisting of the thoracic ganglia as well as abdominal ganglia.

In the Scarabaeoidea a very clear phylogenetic trend can be followed; the more primitive the taxa the longer the connectives between ganglia and the more visible each individual ganglion. Crowson (1981) stated that the nervous system is very useful in the reconstructing

of the phylogeny as there are seldom reversals (Dollo's law).

PHYLOGENETIC INTERPRETATION

Character 6: Position of suboesophageal ganglion:

0 - ganglion situated ventrally against the foregut:

1 - suboesophageal ganglion moved posteriorly

Character 7: Number of thoracic ganglia visible:

0 - all three ganglia visible;

1 - meso- and metathoracic ganglia united;

2 - pro- meso and metathoracic ganglia united

Character 8: Number of abdominal ganglia visible:

0 - all six ganglia visible, first one or two abdominal ganglia fused to metathoracic ganglion; all other abdominal ganglia connected to each other with relatively long connectives;

1 - abdominal ganglia separately visible but connectives absent, the only distinction between ganglia is small holes; the first abdominal ganglion - fused to the metathoracic ganglion;

2 - abdominal ganglia all fused to one another and to the metathoracic ganglion

Structure of the internal female reproductive organs in insects

While the distinction between external and internal genitalia is convenient in males, it is less so in females and it becomes necessary, in the latter, to distinguish between cuticular (ectodermal) and mesodermal structures (Romoser, 1981). The female reproductive system consists of a pair of ovaries that connect with a pair of lateral oviducts. The lateral oviducts join to form a median oviduct opening posteriorly into a genital chamber. Sometimes this genital chamber is closed, forming the vagina. A bursa copulatrix is also present- this duct receives the penis. Opening from the vagina is a spermatheca for the storage of sperm. A spermathecal accessory gland or pair of accessory glands is usually present.

The ovaries of Collembola are not composed of ovarioles, but are sac-like- their ovaries are probably not homologous with other insects (Chapman, 1969). The ovaries lie in the abdomen, each consisting of ovarioles. The number of ovarioles vary, e.g. in Orthoptera there may be anything between eight and 100 ovarioles per ovary, the queen termite possesses over 2000 ovarioles per ovary, Diptera between 10 and 100 and most Lepidoptera possess only four ovarioles per side (Chapman, 1969).

The ovaries each open into a lateral oviduct which in turn opens into a median oviduct. In Dermaptera the median oviduct opens at a gonopore situated ventrally on the posterior end of segment seven. In most other groups the median oviduct opens into a genital chamber invaginated above the sternum of segment 8. Sometimes the genital chamber becomes tubular and is then a continuation of the oviduct through segment 9. This continuation is called the vagina and its external opening, the vulva. It is often not distinguishable in structure from the oviduct, but its anterior end is marked by the insertion of the spermatheca (Snodgrass, 1935). Most female Lepidoptera possess two reproductive openings. One on segment nine that serves for the discharge of eggs and is called the oviporus, while the other is on segment eight and is the copulatory opening or vulva. Two openings also occur in water beetles *Agabus*, *Ilybius* and *Hydroporusm* but both openings are terminal with the opening of the bursa copulatrix immediately above the vaginal opening (Jackson, 1960).

Female accessory glands sometimes are present, arising from the genital chamber or the vagina. Often the function of these glands is to produce a substance for attaching eggs to the substratum during oviposition and are therefore sometimes called colleterial glands. In the genus *Periplaneta* (Blattodea) the eggs are laid in an ootheca, which consists of a cuticle-like substance, produced by these accessory glands. Frothy secretions around the eggs of *Chironomus* (Diptera) and silk which forms an egg cocoon (*Hydrophilus*, Coleoptera) are also produced by accessory glands (Chapman, 1969).

The cuticular structures of typical coleopteran female genitalia consist of the genital chamber, accessory glands, vagina, bursa copulatrix, common oviduct, spermatheca and spermathecal accessory glands (Snodgrass 1935; Matsuda, 1976; Crowson, 1981).

The essential parts of the internal female reproductive organs of Coleoptera consist of a pair of ovaries that consist of a group of polytrophic ovarioles, two lateral oviducts converging posteriorly, forming the median oviduct or the oviductus communis (Bonhag, 1958). This oviductus communis opens into the vagina that in turn opens between the ovipositor lobes (de Wilde & de Loof, 1973a). The bursa copulatrix and spermatheca with spermathecal duct open into the oviductus communis. The oviductus communis sometimes receives openings of glandular structures. They may be paired.

Morphological characters of the internal female reproductive organs of the Scarabaeoidea, and phylogenetic interpretations

GENERAL STRUCTURE

The internal female reproductive organs (from anterior to posterior) of the Scarabaeoidea consist of the following structures:

Two groups of ovarioles, the number varying between the different groups (and discussed in the following paragraphs), opening each into a lateral oviduct. These two lateral oviducti converge forming the median oviduct or the oviductus communis, which is membranous. The oviductus communis opens into the vagina (either membranous or muscular). The vagina lies between plates of the external reproductive organs or the ovipositor (discussed later in the chapter). The bursa copulatrix (the epithelium covering the structure is either membranous or muscular) as well as the duct of the spermatheca and spermathecal gland open into the oviductus communis. The spermatheca and its gland have a variety of forms, differing even between two closely related species, and the outside epithelial layer of the spermatheca and its gland may either be membranous, muscular or sclerotised (which also varies between closely related species). There are sometimes glandular structures (one or two pairs) called accessory glands opening into the oviductus communis. These accessory glands are always membranous.

OVARY NUMBER

Two ovaries are present in all Scarabaeoidea except in the Scarabaeinae, where only 1 is present (Halffter & Matthews, 1966). Sometimes, the second, much reduced ovariole is still present in some members of the Scarabaeinae, e.g. Pinotini (personal observation).

OVARIOLE NUMBER

The most common number of ovarioles found in the Scarabaeoidea is six (Ritcher & Baker, 1977). The number of ovarioles per ovary, however, varies amongst the different groups in the Scarabaeoidea (all references are from Ritcher & Baker (1974), unless otherwise specified): 2 -2 in Passalidae (Williams, 1945); 14-14 to 25-25 in Pleocomidae; 6 -6 in Bolboceratinae (Williams, 1945); 6-6 in Geotrupidae (Halffter & Lopez-Guerrero, 1985; Bovo & Zunino, 1983)); 6-6 in Glaphyridae; 6-6 in Ochodaeidae; 6-6 in Ceratocanthidae; 2, or 3, or 6 in Aphodiinae; 6-6 in Hopliinae; 6-6 in Dynastinae (Williams, 1945; Mathur & Srivastava, 1959); 6-6 in Rutelinae (Williams, 1945); 6-6, 9-9 or 12-12 in Melolonthinae; 6-6 and 12-12 in

Cetoniinae; 6-6 and 12-12 in Trichiinae and 6-6 in Valginae.

Based on commonality, the 6-6 condition in the superfamily appears to be the ancestral one, with the increase or decrease in the number representing derived conditions (Scholtz *et al.*, 1994).

SPERMATHECA AND SPERMATHECAL GLAND

As mentioned in the first paragraph, the outside or epithelial layer of the spermatheca has a tendency to be either membranous in, e.g. Geotrupidae (Halffter & Lopez-Guerrero, 1985), or sclerotised, in for example Scarabaeinae (Heymons, 1930; Halffter & Lopez, 1977).

BURSA COPULATRIX

In the Scarabaeoidea the bursa copulatrix is either a sac-like, elongated protrusion, or flattened. The groups possessing an elongated protrusion are Bolboceratidae (Williams, 1945), Glaphyridae (Ritcher & Baker, 1974), Dynastinae (Williams, 1945; Mathur & Srivastava, 1959) and Melolonthinae (Berberet & Helms, 1972). The bursa copulatrix is flattened, with a few folds in the epithelium in the subfamily Scarabaeinae (Heymons, 1930).

GLANDS

Paired glandular structures sometimes open into the oviductus communis (personal observation). These structures are present only in some of the more derived groups of the superfamily like the Melolonthinae and Cetoniinae (described in detail in the chapters covering the specific groups that possess these glandular structures).

PHYLOGENETIC INTERPRETATION

Character 9: Number of ovaries:

0 - two ovaries per female;

1 - second, but reduced ovary present;

2 - only one ovary per female

Character 10: Number of ovarioles:

0 - six ovarioles per side;

1 – more or less than 6 ovarioles per side

Character 11: Form of the bursa copulatrix:

0 - bursa lengthened;

1 - anterior area of bursa connected to the ventral body wall;

2 - bursa flattened

Character 12: Presence of glandular structures:

0 - glandular structures absent;

1 - one or two pairs of glands present

Character 13: Attachment of spermathecal duct:

0 - spermathecal duct basally attached;

1 - spermathecal duct distally attached

Structure of the internal male reproductive organs in insects

The male reproductive organs in insects typically consist of a pair of testes that connect with paired seminal vesicles and a median ejaculatory duct. In most insects there are also a number of accessory glands that open into either the vasa deferentia or ejaculatory duct. The testes may lie above or below the alimentary canal in the abdomen and are often situated close to the midline. Each testis usually consists of a number of testis tubes or lobes. Sometimes there is only a single follicle (e.g. Coleoptera, Adephaga) while there are two in lice (Phthiraptera), and in short-horned grasshoppers (Acrididae, Orthoptera) there may be over a 100. In members of the Lepidoptera, the follicles are incompletely separated from each other, while the testes of Diptera consist of simple, undivided sacs (Chapman, 1969).

From each testicular follicle there is a fine and thin duct, usually short, called the vas efferens. This duct connects with the vas deferens. Frequently the vasa deferentia are very long, forming a coiled structure called the epididymis (Snodgrass, 1935). The vasa deferentia lead into the distal end of the ejaculatory duct and are often dilated, forming a seminal vesicle.

The male accessory glands open into the vasa deferentia or the distal end of the ductus ejaculatorius. The number of accessory glands varies considerably. Apterygota and some Diptera have none at all. Members of Orthoptera possess 15 pairs.

The internal male reproductive organs of the Coleoptera consist of a paired testis that consist of testicular lobes, vasa efferentia, paired vasa deferentia and seminal vesicles ((Crowson, 1981; Romoser, 1981). Into each seminal vesicle also opens one, two or three pairs of accessory glands. The paired seminal vesicles open into the ductus ejaculatorius (Crowson,

1981; Romoser, 1981).

Each testis of members of the genus *Sphaerites* (Histeridae) possess six elongated testicular lobes, a slender vas deferens and three paired accessory glands (Crowson, 1974). *Hister striola* possesses six or seven elongated sperm-tubes and at least one pair of accessory glands (Crowson, 1974). The male reproductive organs of *Dascillus cervinus* (Dascillidae) consist of five or seven testicular lobes per testis, a pair of vasa deferentia and two pairs of accessory glands. One of the pairs of spermathecal glands is kidney-shaped and fairly large while the other pair is smaller and rounded with deep folds in their walls (Kasap & Crowson, 1975).

Morphological characters of the internal male reproductive organs of Scarabaeoidea, and phylogenetic interpretations

GENERAL STRUCTURE

The internal male reproductive organs of the Scarabaeoidea possess the same as that of a typical insect. The number of testicular lobes varies (discussed in the next paragraphs). There are also accessory glands (either one, two or three pairs), opening into the ductus ejaculatorius. The epithelial layer of these different ducts is always membranous.

NUMBER OF TESTICULAR LOBES

The male has the same number of testicular lobes as the number of ovarioles in its female, with the exception of Scarabaeinae and Glaresidae. In the Scarabaeinae females only possesses one ovariole but males possess four testicular lobes per side (Williams, 1945). Males of the Glaresidae possess 4 testicular lobes per side, while the females possess 6 ovarioles per side (personal observation). The following number of lobes are found in the Scarabaeoidea: 6-6 in Bolboceratidae (Williams, 1945); 6-6 in Dynastinae (Mathur & Srivastava, 1959); 6-6 in Rutelinae (Williams, 1945) and 6-6 in Melolonthinae (Williams, 1945; Berberet & Helms, 1972; Stringer 1990).

Six is, as in the female ovariole number, the most common number (personal observation). The number of testicular lobes shows no definite trend among the different groups and varies even within groups. The most primitive form of the testicular lobes seems to be elongated with the more derived groups possessing more rounded testicular lobes.

ACCESSORY GLANDS

Passalidae (Williams, 1945) and Bolboceratidae (Williams, 1945) possess only one pair of accessory glands, while Melolonthinae (Williams, 1945; Berberet & Helms, 1972; Stringer 1990) and Rutelinae (Anderson, 1950b) possess two pairs of accessory glands. Some of the groups studied possess up to three or four, for example Melolonthinae and Cetoniinae (personal observation).

PHYLOGENETIC INTERPRETATION

Character 14: Number of testicular lobes:

0 - six testicular lobes per side;

1 – more or less than six testicular lobes per side

Character 15: Number of accessory glands:

0 - one pair of accessory glands;

1 - more than one pair of accessory glands

External female reproductive organs: the ovipositor in Coleoptera

In some insects the female has no special structures associated with egg-laying, but in others the posterior part of the abdomen or some of the posterior abdominal appendages are modified to form an ovipositor. The ovipositor enables the female to insert her eggs into different material, e.g. plant or animal tissue, decomposing materials or the ground.

The gonopore or egg opening is usually situated on or behind the 8th or 9th abdominal segment (except in Ephemeroptera and Dermaptera where it is found behind segment seven). In many orders there are no special structures associated with oviposition, although the terminal segments of some insects are sometimes long and telescopic forming a type of ovipositor (Chapman, 1969).

The ovipositor of members of Thysanura, Odonata, Orthoptera, Homoptera, Heteroptera, Thysanoptera and Hymenoptera are derived from appendages of abdominal segments eight and nine. Scudder (1961) believes that *Lepisma* possesses the most basic form of an ovipositor and that the ovipositors of other insects were derived from this basic form. At the base of the ovipositor on each side are the coxae of segments eight and nine. These are known as the first and second gonocoxae (or first and second valvifers). Articulating with

each of these plates is a slender process that curves posteriorly. These are the first and second gonapophyses (or valvulae) and they form the shaft of the ovipositor. In *Lepisma* the second gonapophyses of the two sides are united so that the shaft comprises three elements which fit together to form a tube through which the eggs pass (Chapman, 1969).

Abdominal segment nine and the gonapophyses in female Coleoptera are modified to form the ovipositor. The gonapophyses are two-segmented in typical beetles, and composed of basal coxites and apical styli that are usually setiferous. The coxites articulate basally with the valvifers, or divided 9th sternum. Modifications of the 9th segment and the gonapophyses may be considerable. The modifications are usually associated with differences in the mode of oviposition. Ovipositor types vary according to the substrate in or on which ovipositioning occurs. Elongated ovipositors, usually developed by the elongation of the 9th segment rather than the gonapophyses (usually the proctiger is drawn out at its front angles to form a pair of sclerotised rods and the paraprocts are similarly extended at their upper ends, producing a tube, with the valvifers and gonapophyses at the apex ventrally) are present in woodboring insects whose larvae occur in dead wood (Cerambycidae and Cupedidae). Short, stout ovipositors adapted for digging, occur in Carabidae, members of Silphidae and some other Polyphaga.

Ovipositors that are adapted for cutting into plant material usually possess reduced styli or the styli may be absent. Usually sharp apical parts to the coxites are developed. This is found in members of the Dytiscidae, Dryopidae, Languriidae and Mordellidae. Extremely reduced ovipositors, usually present in insects where eggs are deposited on exposed surfaces, or where the rostrum is used to push them into a pre-formed cavity, are found in Curculionidae, Chrysomelidae, members of the Scarabaeoidea and Heteroceridae (Tanner, 1927, Crowson, 1981).

Complex modifications to the tergites and sternites of abdominal segment 8 are sometimes found, as in the Staphylinidae genus *Tachinus* (Crowson, 1981).

Morphological characters of the ovipositor of Scarabaeoidea, and phylogenetic interpretations

The ovipositor may be present or absent. When present, it consists of various sclerites - the

tergite, pleurites, sternites and hemisternites. The tergite is situated dorsally, above the anus. The paired pleurites are situated laterally; each consisting of two elongated sclerotised plates. Two hemisternites, usually with well-developed styli at their tips, may be present and are situated ventrally. The paired sternites are also situated ventrally. The hemisternites and sternites can be united to each other forming one structure. These paired, united structures are usually quite large (Holloway, 1972).

PHYLOGENETIC INTERPRETATION

Character 16: Presence of ovipositor:

0 - ovipositor present;

1 - ovipositor absent

Character 17: Presence of hemisternites and sternites:

0 - hemisternite and sternite separate;

1 - hemisternite united to sternite forming one enlarged structure;

2 - enlarged structure divided

Character 18: Form of tergite:

0 - tergite undivided;

1 - tergite divided;

2 - tergite divided by membranous area;

3 - tergite completely membranous

4. ALIMENTARY CANAL

Introduction

The general structure and morphology of the alimentary canal were discussed in Chapter 3. Characters as well as the polarity of character states were also determined in Chapter 3. In this chapter, literature (if available) pertaining to individual families, and in the case of Scarabaeidae, subfamilies, are discussed. Morphological descriptions (of species dissected from each taxon - species dissected listed in Appendix 1.1) as well as phylogenetic interpretation of each of the identified characters, follow.

The aims of this chapter are to discuss:

- relevant literature dealing with the morphology of the alimentary canal of each taxon of the Scarabaeoidea
- the morphology of the alimentary canal of each taxon (results from the research done for the thesis)
- phylogenetic trends in the morphology of the alimentary canal for each taxon

Glaresidae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 4.1)

The foregut - divided into a pharynx and oesophagus. Pharynx - clearly thinner than the oesophagus. Cardiac valve - clearly visible and marks the beginning of the midgut. Midgut - short and differentiated into a thinner anterior area and a thicker posterior area. Midgut- covered by numerous small papillae. Pyloric valve - clearly visible and separates the mid- and hindgut. Two pairs of Malpighian tubules arising laterally are present. Hindgut - differentiated into a proximal ileum, distal ileum, colon, rectum and anus. These areas can be distinguished from each other by the difference in thickness (e.g. *Glaresis* (Fig.4.1)).

PHYLOGENETIC INTERPRETATION

(CH1) Pharynx and oesophagus distinguishable - 0;

(CH2) midgut short - 0;

(CH3) midgut differentiated into anterior and posterior region - 0;

(CH4) two pairs of Malpighian tubules attached laterally - 0;

(CH5) hindgut differentiated into proximal ileum, distal ileum, colon and rectum - 0.

Passalidae

LITERATURE REVIEW

Lewis (1926) and Patterson (1937) described the gross anatomy as well as the histology of the digestive tract of *Passalus cornutus*. The foregut is comparatively simple, consisting of the buccal cavity, a very short pharynx and a short oesophagus. The midgut is coiled, covered by numerous small papillae and separated from the foregut by a constriction composed of two distinct rings. The mid- and hindgut are separated by the pyloric valve. Four Malpighian tubules are attached at a single place at the point of transition from the mid- to the hindgut. The hindgut is divided into four regions, the short proximal (appearing the same as the midgut but without papillae) and longer distal ileum (characterised by numerous folds of the wall; one of the folds in the wall is an enlargement forming an intestinal caecum), colon (a long slender tube) and short, enlarged rectum. In the region of the transition between the ileum and the colon, there is a fold in the wall of the tract that is considered as an intestinal valve.

The alimentary canal of *Odontotaenius disjunctus* was described by Patterson (1937). The foregut is divided into the pharynx, oesophagus and crop, and these two areas (oesophagus and crop) separated by a muscular stricture. The rest of alimentary canal corresponds with that of *P. cornutus*.

DESCRIPTION (FIG.4.2 - 4.4)

Foregut differentiated into two areas - pharynx and oesophagus. Anterior area (pharynx) - thin. Thicker oesophagus terminates in oesophageal valve - situated between the fore- and midgut. Oesophagial valve - clearly visible. Midgut - short and undifferentiated, covered by small papillae. Pyloric valve situated between mid- and hindgut. Four Malpighian tubules present - two on each side. Hindgut - differentiated into five areas: a thin, smooth proximal ileum; a thicker distal ileum; thin, smooth colon; rectum and anus. Distal ileum - clearly distinguishable by six large longitudinal thickenings. Finger shaped cacae - present on the margin between the distal and proximal ileum in all specimens studied (e.g. *Odontotaenius disjunctus* (Fig. 4.2) and *Passalus punctiger* (Fig. 4.3), except *Ogyges marilucasae* (Fig. 4.4)). Colon - widens slightly into a very short rectum that terminates in the anus.

PHYLOGENETIC INTERPRETATION

(CH1) Pharynx and oesophagus distinguishable - 0;

(CH2) midgut short - 0;

(CH3) midgut not differentiated into anterior and posterior region - 1;

(CH4) two pairs of Malpighian tubules attached laterally - 0;

(CH5) hindgut differentiated into proximal ileum, distal ileum, colon, rectum and anus – 0.

Lucanidae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 4.5; 4.6)

Foregut - divided into two parts, pharynx, long and thin; oesophagus - thicker. Cardiac valve separates the fore- and midgut, not very prominent - appears as a slight invagination. First part of the midgut - thin, widening into a bulbous area. Midgut - rather short, covered with small papillae. Malpighian tubules mark the beginning of the hindgut. Two pairs arranged laterally are present. Pyloric valve situated between the mid- and hindgut - not prominent. Hindgut - not differentiated; appearing as a long, thin and undifferentiated duct (e.g. *Syndesus cornutus* and *Prosopocoilus natalensis* (Fig. 4.5)); or differentiated into proximal ileum, distal ileum, colon and rectum (e.g. *Platyceropsis* sp., *Ceruchus* sp. and *Sinodendron rugosum* (Fig. 4.6)).

PHYLOGENETIC INTERPRETATION

(CH1) Pharynx and oesophagus distinguishable - 0;

(CH2) midgut short - 0;

(CH3) midgut differentiated into anterior and posterior region - 0;

(CH4) two pairs of Malpighian tubules attached laterally - 0;

(CH5) hindgut differentiated into proximal ileum, distal ileum, colon and rectum (*S. rugosum*, *Platyceropsis* sp. and *Ceruchus* sp.) - 0;

hindgut not differentiated into proximal ileum, distal ileum, colon and rectum (long, thin and undifferentiated) - 1.

Diphyllostomatidae

No literature available.

No fresh specimens were dissected.

Glaphyridae

No literature available.

No fresh specimens were dissected.

Trogidae

LITERATURE REVIEW

No literature available.

DESCRIPTION (Fig. 4.7)

Foregut - differentiated into a long, thin pharynx. Oesophagus - short and thick. Cardiac valve - prominent; separates the fore- and midgut. Midgut - not differentiated into different areas. Midgut - covered with numerous small papillae. Pyloric valve - separates the mid- and hindgut. Two pairs of Malpighian tubules - open laterally. Malpighian tubules - present on the margin between the mid- and hindgut. Hindgut - clearly differentiated into a long, thin proximal ileum, a bulbous distal ileum, colon, rectum and anus (e.g. *Polynoncus pedestris* (Fig. 4.7)).

PHYLOGENETIC INTERPRETATION

(CH1) Pharynx and oesophagus distinguishable - 0;

(CH2) midgut short - 0;

(CH3) midgut not differentiated into anterior and posterior region - 1;

(CH4) two pairs of Malpighian tubules attached laterally - 0;

(CH5) hindgut differentiated into proximal ileum, distal ileum, colon and rectum - 0.

Bolboceratidae

LITERATURE REVIEW

No literature available.

DESCRIPTION (Fig. 4.8)

Foregut - not differentiated into a pharynx and oesophagus (e.g. *Bolbocaffer* sp. (Fig. 4.8)). Foregut - short; separated from the midgut by the cardiac valve. Cardiac valve - clearly visible. Midgut - undifferentiated and short. Midgut - separated from the hindgut by the pyloric valve. Four Malpighian tubules - situated on the margin of the mid- and hindgut. Four tubules open two-two on each lateral side. Hindgut - differentiated into the short, smooth distal ileum; wider, striated proximal ileum; colon; rectum and anus.

PHYLOGENETIC INTERPRETATION

(CH1) Pharynx and oesophagus indistinguishable - 1;

(CH2) midgut short - 0;

(CH3) midgut not differentiated into anterior and posterior region - 1;

(CH4) two pairs of Malpighian tubules attached laterally - 0;

(CH5) hindgut differentiated into proximal ileum, distal ileum, colon, rectum and anus - 0.

Pleocomidae

LITERATURE REVIEW

No literature available.

DESCRIPTION (Fig. 4.9)

Foregut - long and thin. No distinction can be made between the pharynx and the oesophagus. Midgut - very short and clearly separated from the foregut by the cardiac valve. Midgut - covered by numerous small papillae. Pyloric valve - separates the mid- and hindgut. Two pairs of Malpighian tubules - open laterally. Hindgut - differentiated into a proximal and distal ileum, colon, rectum and anus (e.g. *Pleocoma shostensis* (Fig. 4.9)).

PHYLOGENETIC INTERPRETATION

(CH1) Pharynx and oesophagus indistinguishable - 1;

(CH2) midgut short - 0;

(CH3) midgut not differentiated into anterior and posterior region - 1;

(CH4) two pairs of Malpighian tubules attached laterally - 0;

(CH5) hindgut differentiated into proximal ileum, distal ileum, colon, rectum and anus - 0.

Geotrupidae

LITERATURE REVIEW

No literature available.

DESCRIPTION (Fig. 4.10; 4.11)

Foregut (of all the subfamilies) - short, not differentiated into the pharynx and oesophagus. fore- and midgut - separated by the cardiac valve. Taurocerastinae - midgut short (e.g. *Taurocerastes* sp. (Fig. 4.10)); of uniform thickness. Geotrupinae - midgut - very long (e.g. *Geotrupes spiniger* (Fig. 4.11)) (as found in the Scarabaeinae); not differentiated. Hindgut - separated from the midgut by the pyloric valve. Four Malpighian tubules - situated on the margin between mid-and hindgut. Tubules - open two-two laterally. Hindgut - differentiated

into a smooth distal ileum; striated proximal ileum; colon, rectum and anus.

PHYLOGENETIC INTERPRETATION

(CH1) Pharynx and oesophagus indistinguishable - 1;

(CH2) midgut short - 0; to long - 1;

(CH3) midgut not differentiated into anterior and posterior region - 1;

(CH4) two pairs of Malpighian tubules attached laterally - 0;

(CH5) hindgut differentiated into proximal ileum, distal ileum, colon, rectum and anus - 0.

Ochodaeidae

No literature available.

No fresh specimens were dissected.

Ceratocanthidae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 4.12)

Foregut - differentiated into a pharynx and oesophagus. Cardiac valve - separates fore- and midgut. Midgut - undifferentiated; covered completely by small papillae. Pyloric valve - separates the mid- and hindgut. Four Malpighian tubules - present; enter gut two-two laterally. Hindgut - clearly separated into the proximal and distal ileum, the colon, rectum and anus (e.g. Ceratocanthidae sp. (Fig. 4.12)).

PHYLOGENETIC INTERPRETATION

(CH1) Pharynx and oesophagus indistinguishable - 1;

(CH2) midgut short - 0;

(CH3) midgut not differentiated into anterior and posterior region - 1;

(CH4) two pairs of Malpighian tubules attached laterally - 0;

(CH5) hindgut differentiated into proximal ileum, distal ileum, colon, rectum and anus - 0.

Hybosoridae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 4.13)

Foregut - short, not differentiated into different areas; of uniform thickness. Cardiac valve-

situated between the fore- and midgut. Midgut - divided into two areas, the anterior region - thicker and wider than the posterior area. Foregut - covered by numerous small papillae. Hindgut - separated from the midgut by the pyloric valve. Four Malpighian tubules - situated two-two laterally. Hindgut - divided into the proximal and distal ileum, the colon, rectum and anus (e.g. *Hybosorus illigeri* (Fig. 4.13)).

PHYLOGENETIC INTERPRETATION

(CH1) Pharynx and oesophagus indistinguishable - 1;

(CH2) midgut short - 0;

(CH3) midgut differentiated into anterior and posterior region - 0;

(CH4) two pairs of Malpighian tubules attached laterally - 0;

(CH5) hindgut differentiated into proximal ileum, distal ileum, colon, rectum and anus - 0.

Scarabaeidae: Aphodiinae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 4.14)

Foregut - short but differentiated into a thin pharynx and a short, bulbous oesophagus. Fore- and hindgut - separated by the cardiac valve (clearly visible). Midgut - short; divided into a thicker anterior area and a thinner posterior area. Entire midgut - covered by numerous small papillae. Mid- and hindgut - separated by the pyloric valve. Four Malpighian tubules - arranged two-two laterally. Hindgut - divided into the proximal and distal ileum, the enlarged colon, rectum and anus (e.g. *Aphodius septemmaculatus* (Fig. 4.14)).

PHYLOGENETIC INTERPRETATION

(CH1) Pharynx and oesophagus distinguishable - 0;

(CH2) midgut short - 0;

CH3) midgut differentiated into anterior and posterior region - 0;

(CH4) two pairs of Malpighian tubules attached laterally - 0;

(CH5) hindgut differentiated into proximal ileum, distal ileum, colon, rectum and anus - 0.

Scarabaeidae: Scarabaeinae

LITERATURE REVIEW

Becton (1930) described the alimentary canal of *Phanaeus vindex* (Phaneini). It is a simple, structure forming eight coils in the abdominal cavity. There are three distinct regions, the

foregut consisting of the buccal cavity which is continuous with the pharynx and oesophagus. The oesophageal valve separates the fore- and midgut. Becton (1930) could detect no crop. The midgut is a long, coiled structure possessing numerous papillae. The four Malpighian tubules arise at the posterior end of the midgut. The pyloric valve is a band-like constriction between the mid- and hindgut. The ileum is slightly widened followed by the rectum (with the greatest diameter of any part of the canal) and anus.

DESCRIPTION (FIG. 4.15)

Foregut - short and of uniform thickness. Midgut - separated from the foregut by the cardiac valve. Cardiac valve - clearly visible. Midgut - very long; curled eight times in the abdominal cavity. Midgut - undifferentiated, of uniform thickness; covered by numerous papillae. Hindgut - separated from the midgut by the pyloric valve. Pyloric valve - not clearly distinguishable. Two pairs of Malpighian tubules - attached laterally - on the margin of the mid- and hindgut. Hindgut - not differentiated into different areas; of uniform thickness; only widens very slightly at the proximal end, presumably forming the rectum (e.g. *Copris* sp. (Fig.4.15)).

PHYLOGENETIC INTERPRETATION

(CH1) Pharynx and oesophagus indistinguishable - 1;

(CH2) midgut very long - 1;

(CH3) midgut not differentiated into anterior and posterior region - 1;

(CH4) two pairs of Malpighian tubules attached laterally - 0;

(CH5) hindgut not differentiated into proximal ileum, distal ileum, colon, rectum and anus - 1.

Scarabaeidae: Melolonthinae

LITERATURE REVIEW

The alimentary canal of *Phyllophaga gracilis* was discussed by Fletcher (1930). The alimentary canal of the beetle is divided into three regions. The foregut consists of the pharynx just posterior of the mouth, the short, narrow oesophagus and the crop that is present as a dilation of the posterior portion of the oesophagus. The oesophageal valve marks the separation between the fore- and midgut. The midgut is a straight tube, nearly uniform in diameter. The mid- and hindgut are separated by the pyloric valve. It is visible as a constriction just before the four Malpighian tubules. Two of the tubes arise from a common opening, while the other two arise separately. The hindgut consists of the proximal and distal ileum. The proximal ileum is short and appears the same as the posterior region of the

midgut but the distal ileum is much larger and conspicuous. The anterior margin of this distal ileum is well defined and rises abruptly from the constriction of the proximal ileum. The colon follows the ileum and is a small tube linking the ileum to the rectum that is an enlargement of the colon. The alimentary canal of *Pyllophaga anxia* has the same morphology as that of *P. gracilis* (Berberet & Helms, 1972).

Lison (1938) described the Malpighian tubules of *Melolontha melolontha*. According to the author two of the four tubules have a common opening into the alimentary canal. He calls them the *"tubes courts"*. These tubules are shorter than the other pair and lie loose in the body cavity. The posterior region of the tubule is inserted onto the hindgut. The other two tubules, the *"tubes longs"* are each inserted laterally and cling to the wall of the canal, turning posteriorly at the oesophageal valve to insert on the hindgut. Both pairs of tubules are smooth at their insertion point, but the wall becomes lace-like with many spherical lobes protruding from its surface. Posteriorly, the tubule wall again appears smooth (this is near its tip).

The alimentary canal of *Diplotaxa liberta* (Jones, 1940) possess the general Melolonthinae structure previously discussed, but the hindgut differs a little. There are four Malpighian tubules, two attaching anterior and the other two posterior of the pyloric valve. The two anterior tubules are ventro-laterally attached, while the other two tubules empty close together into a bladder-like structure situated on the dorsal side of the anterior end of the ileum. The dorsal tubules are very long and extend to the oesophageal valve.

DESCRIPTION (FIG. 4.16)

Foregut - differentiated into a thinner pharynx and a thicker oesophagus. Fore- and hindgut - separated by a clearly distinguishable cardiac valve. Midgut - short but not differentiated into a proximal and distal area; separated from the hindgut by the clearly visible pyloric valve. Four Malpighian tubules - present; two of the four - entering the alimentary canal laterally; attachment position of the other two tubules - moved anteriorly. Hindgut - clearly differentiated into a thin, smooth distal ileum, a thicker proximal ileum, rectum and anus. Ileum - possess striations on the wall (e.g. Melolonthinae sp. (Fig. 4.16)).

PHYLOGENETIC INTERPRETATION

(CH1) Pharynx and oesophagus distinguishable - 0;

(CH2) midgut short - 0;

(CH3) midgut not differentiated into anterior and posterior region - 1;

(CH4) four Malpighian tubules present, two attached laterally, position of attachment of other two moved anteriorly - 1;

(CH5) hindgut differentiated into proximal ileum, distal ileum, colon, rectum and anus - 0.

Scarabaeidae: Rutelinae

LITERATURE REVIEW

The anatomy and physiology of the alimentary canal of *Popillia japonica* were discussed by Swingle (1930). The foregut is thread-like with the posterior half widening into a pear-shaped bulb. Between the fore- and midgut lies the very small oesophageal valve. The midgut is of uniform diameter and constitutes the major part of the alimentary canal and its surface is covered by minute, knob-like papillae. The four Malpighian tubules are situated just anterior of the pyloric valve. Two tubules cling to the wall of the alimentary canal and run posteriorly to the colon while the remaining two are about half the length of the first and have a common opening into the gut. The walls of all four tubules are smooth as they leave the gut but appear lace-like as each tube possesses many spherical lobes protruding from its surface. Beyond the pyloric valve the ileum is slightly widened with its wall wrinkled and pitted. The hindgut narrows near the middle for a short distance after widening again into the large rectum, terminating in the anus.

INTERPRETATION (FIG. 4.17; 4.18)

Foregut - differentiated into a narrow pharynx and a bulbous oesophagus. Fore- and midgut - clearly separated by the cardiac valve. Midgut of three species studied (Rutelinae from Pretoria and from Richards Bay (Fig. 4.17)) - short and differentiated into two distinct areas, a wider proximal area and a distal area that is narrower. All other species - undifferentiated midgut of uniform thickness (e.g. *Anomala* sp. (Fig. 4.18)). Midgut - covered by small papillae. Hindgut - separated from the midgut by the pyloric valve. Four Malpighian tubules - present, two opening laterally and the other two opening together anteriorly. Hindgut - clearly differentiated into a thin, smooth distal ileum, a thicker proximal ileum, a rather long, narrow rectum and anus.

PHYLOGENETIC INTERPRETATION

(CH1) Pharynx and oesophagus distinguishable - 0;

(CH2) midgut short - 0;

(CH3) midgut differentiated into anterior and posterior region - 0, or not differentiated into

anterior and posterior region - 1;

(CH4) four Malpighian tubules present, two attached laterally, position of attachment of other two moved anteriorly - 1;

(CH5) hindgut differentiated into proximal ileum, distal ileum, colon. rectum and anus - 0.

Scarabaeidae: Hopliinae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 4.19)

Foregut - divided into a narrow pharynx and a bulbous oesophagus. Fore- and midgut - separated by the cardiac valve. Midgut - short; of uniform length; covered by numerous small papillae. Mid- and hindgut - divided by the pyloric valve. Four Malpighian tubules - present, two opening laterally and the other two opening together anteriorly. Hindgut - differentiated into different areas; difficult to distinguish between the proximal ileum, colon and the rectum (Fig. 4.19).

PHYLOGENETIC INTERPRETATION

(CH1) Pharynx and oesophagus distinguishable - 0;

(CH2) midgut short - 0;

(CH3) midgut not differentiated into anterior and posterior region - 1;

(CH4) four Malpighian tubules present, two attached laterally, position of attachment of other two moved anteriorly - 1;

(CH5) hindgut differentiated into proximal ileum, distal ileum, colon, rectum and anus - 0.

Scarabaeidae: Dynastinae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 4.20)

Foregut - consists of pharynx and oesophagus (not clearly differentiated). Fore- and midgut - separated by the cardiac valve that is clearly visible. Midgut - short and undifferentiated; covered by numerous small papillae. Pyloric valve - separates the mid- and hindgut. Four Malpighian tubules - present; two opening laterally; other two opening together anteriorly on the hindgut. Hindgut - clearly differentiated into the short, smooth distal ileum bulbous proximal ileum, long colon, rectum and anus (e.g. Dynastinae sp. (Fig. 4.20)).

PHYLOGENETIC INTERPRETATION

(CH1) Pharynx and oesophagus distinguishable - 0;

(CH2) midgut short - 0;

(CH3) midgut not differentiated into anterior and posterior region - 1;

(CH4) four Malpighian tubules present, two attached laterally, position of attachment of other two moved anteriorly - 1;

(CH5) hindgut differentiated into proximal ileum, distal ileum, colon, rectum and anus - 0.

Scarabaeidae: Cetoniinae

LITERATURE REVIEW

Cheung & Low (1975) investigated the ultrastructure of the midgut of *Protaetia acuminata*. In this beetle the midgut is not differentiated into different regions and papillae are present.

DESCRIPTION (FIG. 4.21)

Foregut - of uniform thickness; without any definite distinction between the pharynx and the oesophagus. Cardiac valve - not clearly distinguishable. Beginning of the midgut - marked by the appearance of small papillae that covers this entire area. Midgut - not divided into different areas; of uniform thickness. Pyloric valve - separates midgut from the hindgut. Malpighian tubules - situated on the margin between mid-and hindgut. Two of the tubules enters the hindgut laterally; other two at the same entrance anteriorly. Hindgut - clearly divided into five areas, a smooth thin distal ileum, a thicker, striated proximal ileum, the colon, slightly enlarged rectum and the anus (e.g. *Hypselogenia geotrupina* (Fig.4.21)).

In one of the species *Ichnestoma stobbiae*, the midgut is extremely shortened (adult members of this species only live a very short time and do not feed).

PHYLOGENETIC INTERPRETATION

(CH1) Pharynx and oesophagus not distinguishable - 1;

(CH2) midgut short - 0;

(CH3) midgut not differentiated into anterior and posterior region - 1;

(CH4) four Malpighian tubules present, two attached laterally, position of attachment of other two moved anteriorly - 1;

(CH5) hindgut differentiated into proximal ileum, distal ileum, colon, rectum and anus - 0.

Scarabaeidae: Trichiinae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 4.22)

Foregut - differentiated into a pharynx and oesophagus; of uniform length and separated from the midgut by the cardiac valve. Midgut - short, of uniform length; covered by numerous small papillae. Mid- and hindgut - separated by the pyloric valve. Four Malpighian tubules - present; two entering laterally; other two opening together anteriorly. Hindgut - divided into the narrow and smooth distal ileum, the wider, bulbous and striated proximal ileum, colon, rectum and anus (e.g. *Campulipus limbatus* (Fig. 4.22)).

PHYLOGENETIC INTERPRETATION

(CH1) Pharynx and oesophagus not distinguishable - 1;

(CH2) midgut short - 0;

(CH3) midgut not differentiated into anterior and posterior region - 1;

(CH4) four Malpighian tubules present, two attached laterally, position of attachment of other two moved anteriorly - 1;

(CH5) hindgut differentiated into proximal ileum, distal ileum, colon, rectum and anus - 0.

Scarabaeidae: Valginae, Oncerinae, Chasmatopterinae and Orphninae

No literature available.

No fresh specimens were dissected.

PLATE 1

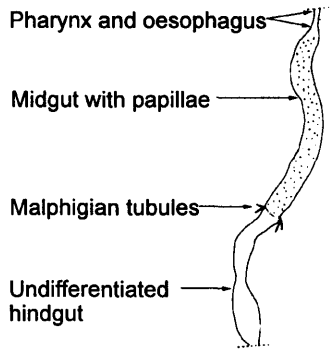


Fig. 4.1

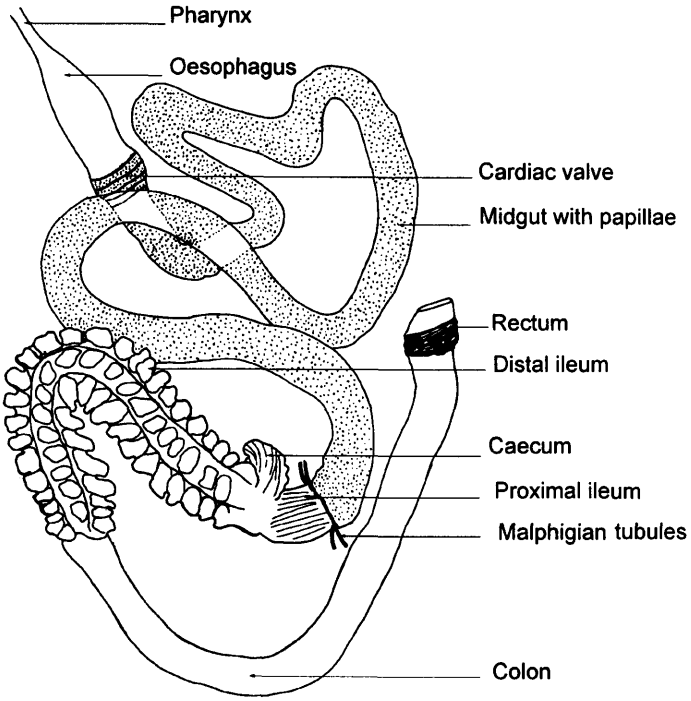


Fig. 4.2

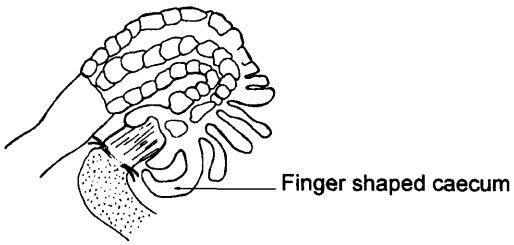


Fig. 4.3

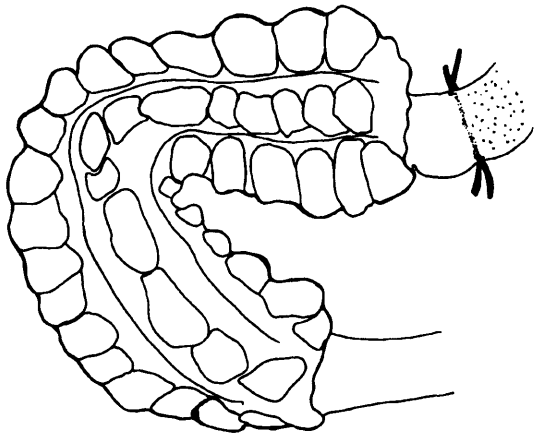


Fig. 4.4

Fig. 4.1 Alimentary canal of a *Glaresis* species (Glaresidae)
Fig. 4.2 Alimentary canal of *Odontotaenius disjunctus* (Passalidae)
Fig. 4.3 Fingershaped caecae (on alimentary canal) of *Passalus punctiger* (Passalidae)
Fig. 4.4 Hindgut of *Ogyges mariculacea* (Passalidae)
Drawings not to scale

PLATE 2

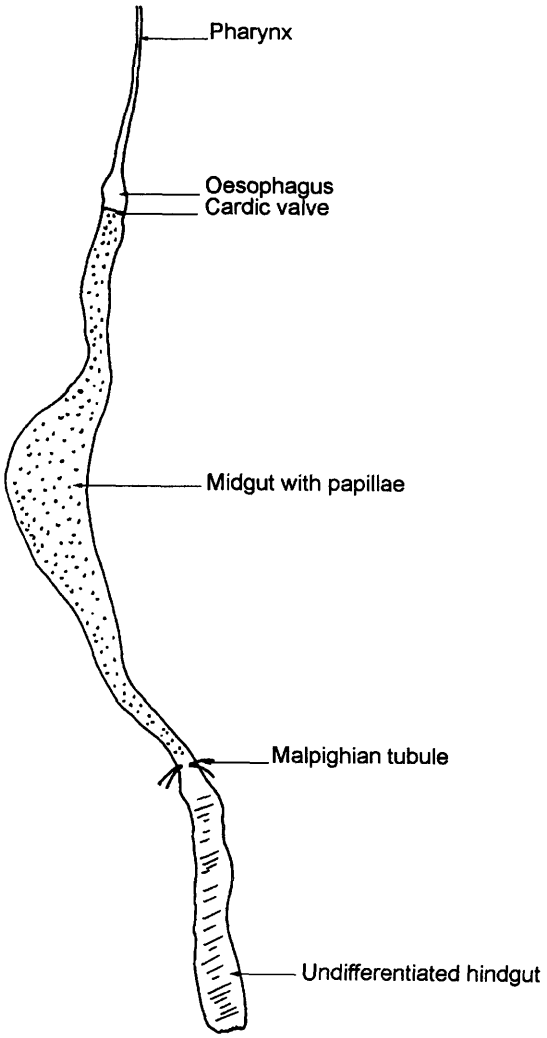


Fig. 4.5

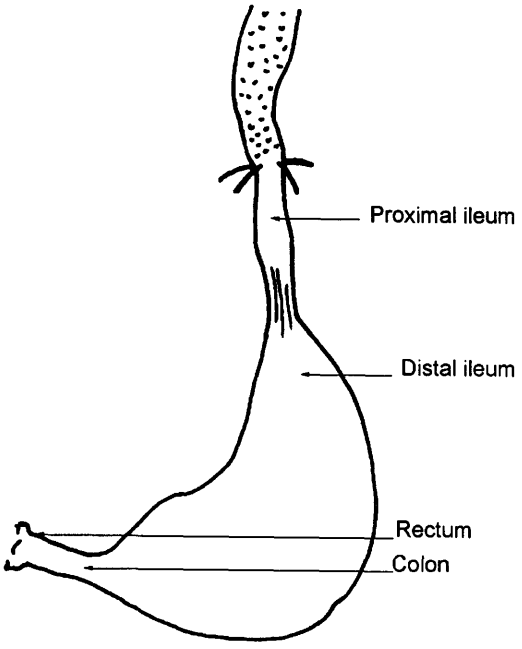


Fig. 4.6

Fig. 4.5 Alimentary canal of *Prosopocoilus natalensis* (Lucanidae)
Fig. 4.6 Hindgut of *Sinodendron rugosum* (Lucanidae)
Drawings not to scale

PLATE 3

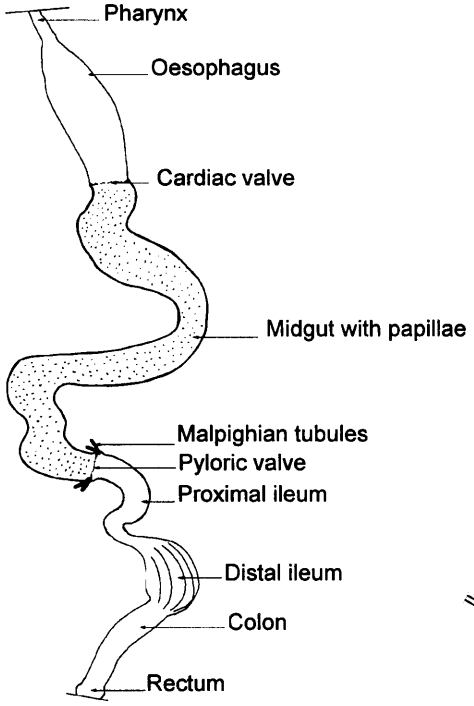


Fig. 4.7

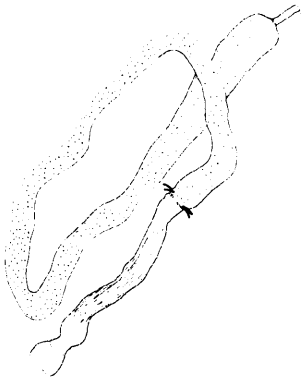


Fig. 4.8

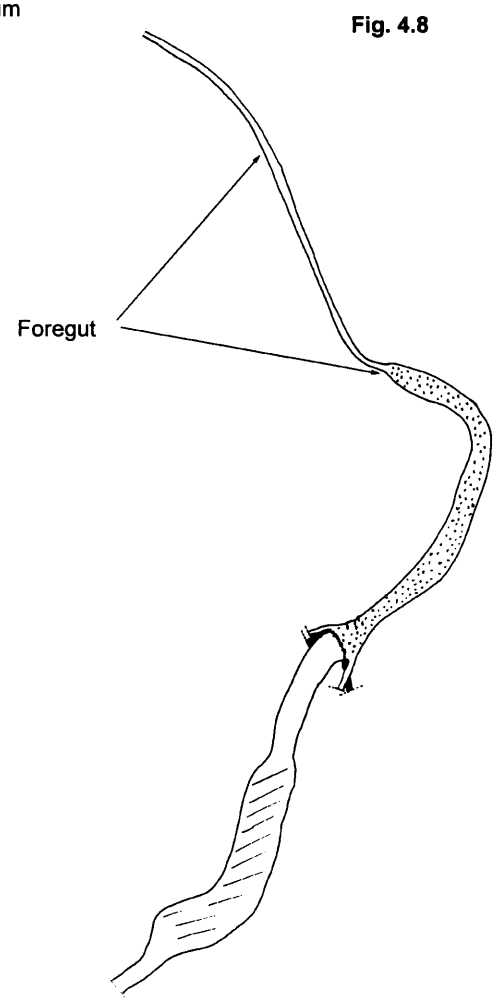


Fig. 4.9

Fig. 4.7 Alimentary canal of *Polynoncus pedestris* (Trogidae)
Fig. 4.8 Alimentary canal of a *Bolbocaffer* species (Bolboceratidae)
Fig. 4.9 Alimentary canal of *Pleocoma shostensis* (Pleocomidae)
Drawings not to scale

PLATE 4

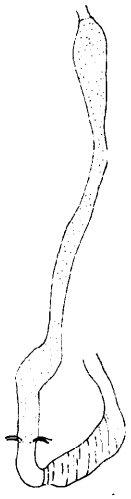


Fig. 4.10

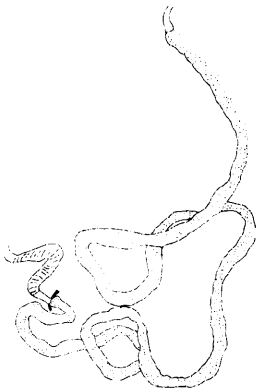


Fig. 4.11

Fig. 4.10 Alimentary canal of a Taurocerastinae species (Geotrupidae)
Fig. 4.11 Alimentary canal of *Geotrupes spiniger* (Geotrupidae)
Drawings not to scale

PLATE 5

Fig. 4.12

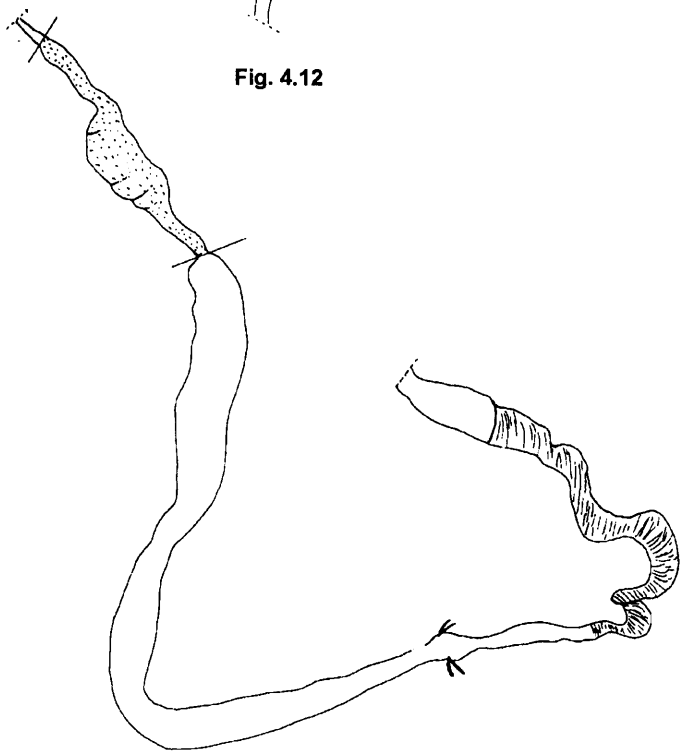


Fig. 4.13

Fig. 4.12 Alimentary canal of a species of Ceratocanthidae
Fig. 4.13 Alimentary canal of *Hybosorus illigeri* (Hybosoridae)
Drawings not to scale

PLATE 6

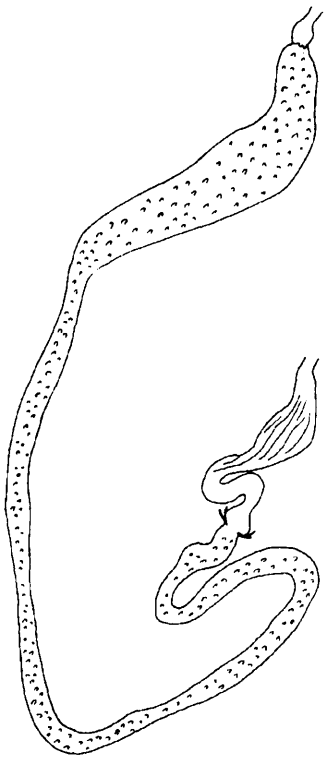


Fig. 4.14

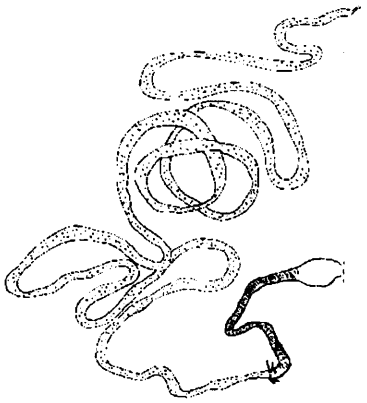


Fig. 4.15

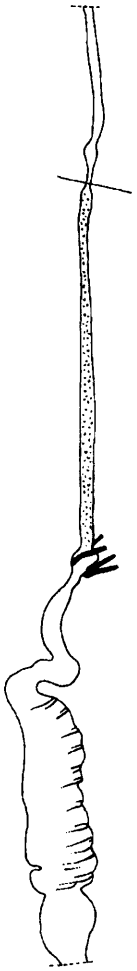


Fig. 4.16

Fig. 4.14 Alimentary canal of *Aphodius septemmaculatus* (Aphodiinae)
Fig. 4.15 Alimentary canal of a *Copris* species (Scarabaeinae)
Fig. 4.16 Alimentary canal of an unidentified Melolonthinae species
Drawings not to scale

PLATE 7

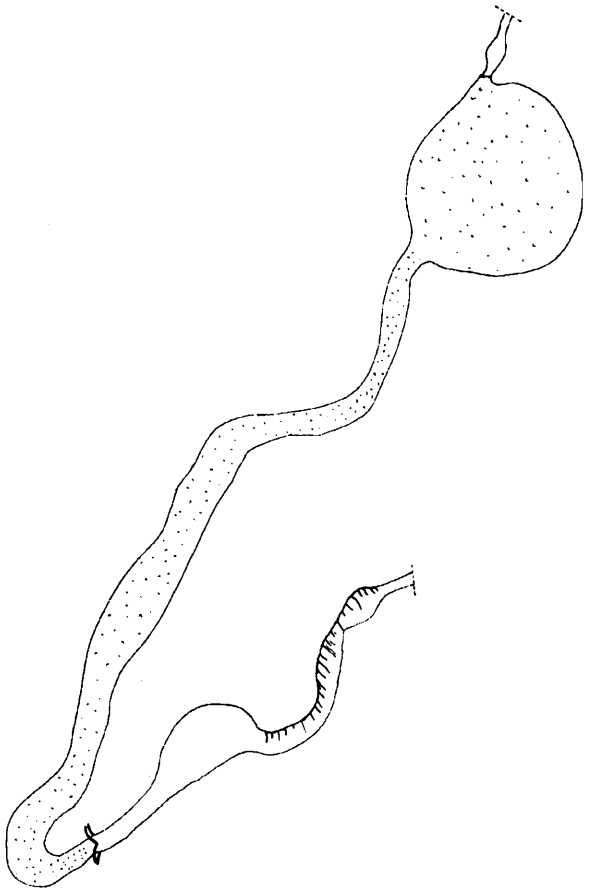


Fig. 4.17.

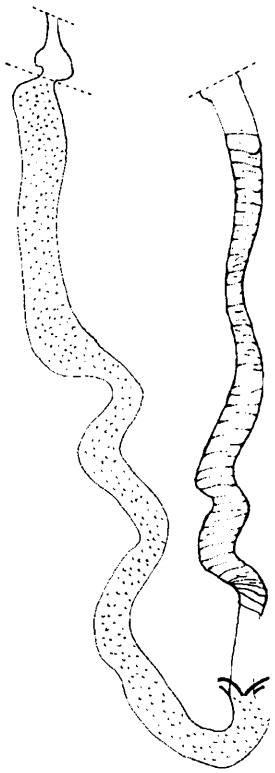


Fig. 4.18

Fig. 4.17 Alimentary canal of a Rutelinae species from Richards Bay
Fig. 4.18 Alimentary canal of an *Anomala* species (Rutelinae)
Drawings not to scale

PLATE 8

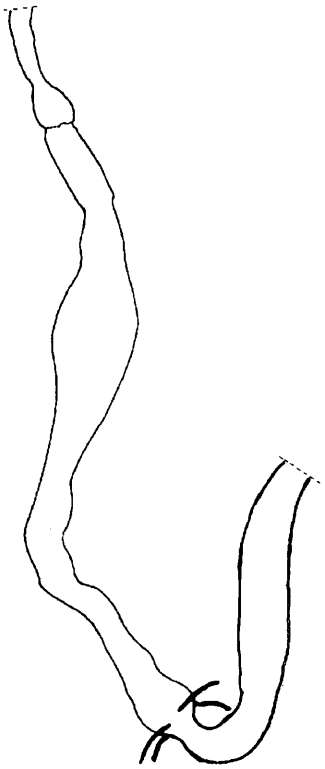


Fig. 4.19

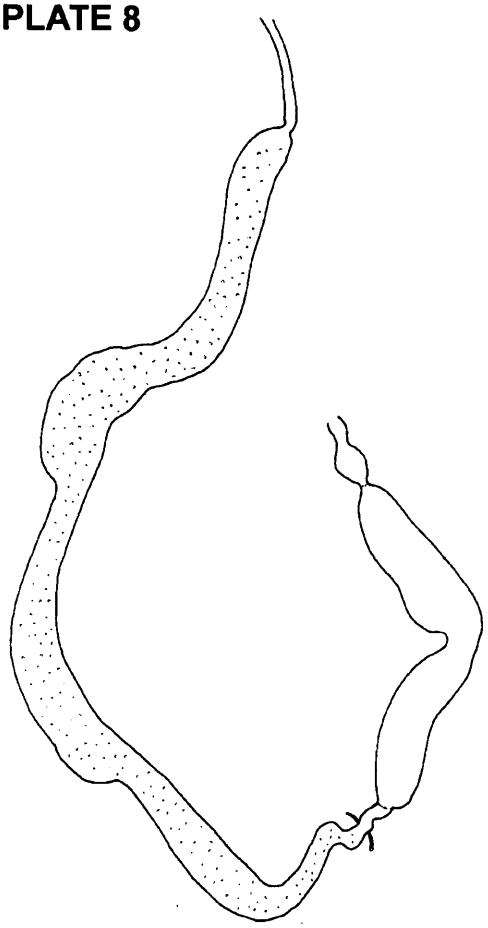


Fig. 4.20

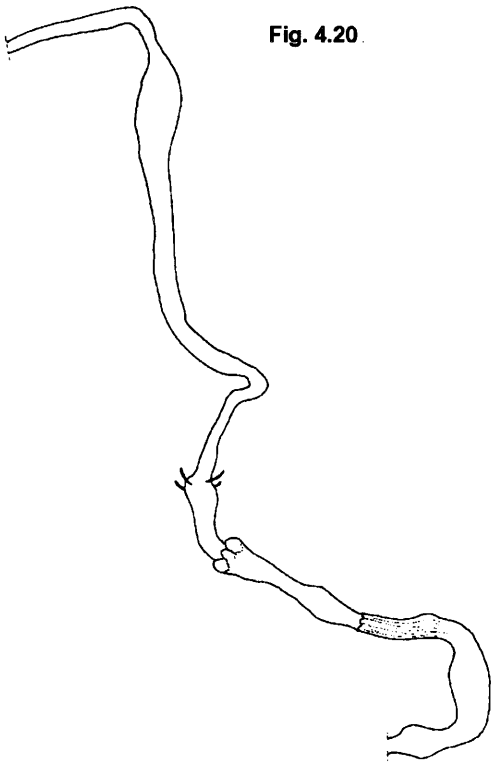


Fig. 4.21

Fig. 4.19 Alimentary canal of an unidentified Hopliinae species
Fig. 4.20 Alimentary canal of an unidentified Dynastinae species
Fig. 4.21 Alimentary canal of *Hypselogenia geotrupina* (Cetoniinae)
Drawings not to scale

PLATE 9

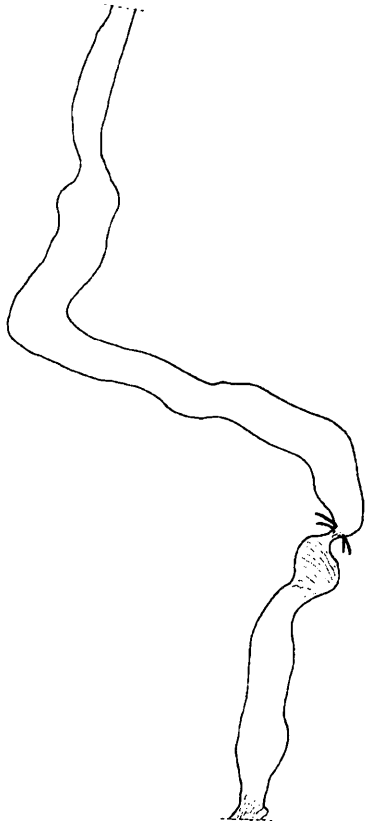


Fig. 4.22

Fig. 4.22 Alimentary canal of *Campulipus limbatus* (Trichiinae)

5. NERVOUS SYSTEM

Introduction

The general structure and morphology of the nervous system were discussed in Chapter 3. Characters as well as the polarity of character states were also determined in Chapter 3. In this chapter, literature (if available) pertaining to individual families, and in the case of Scarabaeidae, subfamilies, are discussed. Morphological descriptions (of species dissected from each taxon - species dissected listed in Appendix 1.1) as well as phylogenetic interpretation of each of the identified characters, follow.

The aims of are chapter is to discuss:

- relevant literature dealing with the morphology of the nervous system of each taxon of the Scarabaeoidea
- the morphology of the nervous system of each taxon (results from the research done for the thesis)
- phylogenetic trends in the morphology of the nervous system for each taxon

Glaresidae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 5.1)

Suboesophageal ganglion - situated on the margin of the head and thorax; separated from the prothoracic ganglion by long connectives. Mesothoracal, metathoracal and abdominal ganglia - all fused to each other. No connectives are visible. Meso- and metathoracic ganglia - clearly distinguishable from each other. Separate abdominal ganglia cannot be distinguished from one another. Abdominal ganglia appear as a single elongated ganglionic mass (e.g. *Glaresis* (Fig. 5.1)).

PHYLOGENETIC INTERPRETATION

(CH6) Suboesophageal ganglion situated ventrally against the foregut - 0;

(CH7) all three thoracic ganglia visible - 0;

(CH8) abdominal ganglia fused to metathoracic ganglion and to each other – 2.

Passalidae

LITERATURE REVIEW

Cody & Gray (1938) studied the nervous system of *Passalus cornutus* and found that it shows a pronounced degree of concentration. The suboesophageal ganglion is separated from the prothoracic ganglion by rather long connectives. The prothoracic ganglion is also separated from the mesothoracic ganglion by long connectives. The meso- and metathoracic ganglia are separated by very short connectives, while the metathoracic and abdominal ganglia are fused (the metathoracic ganglion is, however, distinguishable).

DESCRIPTION (FIG. 5.2)

Suboesophageal ganglion - situated on the margin between the head and thorax, close to the pharynx. Prothoracic ganglion - connected to the suboesophageal ganglion by long connectives. Prothoracic ganglion - connected to the meso- meta- and abdominal ganglionic mass by long connectives. Meso- and metathoracic ganglia - visible as two separate ganglia, no connectives are present. Abdominal ganglia - fused together and connected to the metathoracic ganglion, no connectives are visible (e.g. *Odontotaenius disjunctus* (Fig. 5.2)). Separate abdominal ganglia are distinguishable only by the small holes left by the remains of the connectives as they shortened during evolution.

PHYLOGENETIC INTERPRETATION

(CH6) Suboesophageal ganglion situated ventrally against the foregut - 0;

(CH7) all three thoracic ganglia visible - 0;

(CH8) all six abdominal ganglia visible, but connectives absent, only distinction between ganglia is small indents. First abdominal ganglion fused to metathoracic ganglion - 1.

Lucanidae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 5.3; 5.4)

Suboesophageal ganglion - situated on the margin of the head and thorax, posterior to the pharynx. Suboesophageal ganglion - connected with the prothoracic ganglion by long connectives. Mesothoracic ganglion - connected with prothoracic ganglion by long connectives. Mesothoracic ganglion - connected with the metathoracic ganglion by very short (but still visible) connectives. In *Prosopocoilus natalensis* and *Figulus* sp. (Fig. 5.3) - first abdominal ganglion - fused to the metathoracic ganglion. In all other freshly killed

specimens studied - first two abdominal ganglia fused with the metathoracic ganglion (e.g. *Syndesus cornutus* (Fig. 5.4)).

PHYLOGENETIC INTERPRETATION

(CH6) Suboesophageal ganglion situated ventrally against the foregut - 0;

(CH7) all three thoracic ganglia visible - 0;

(CH8) first one or two abdominal ganglia fused to metathoracic ganglia, last four or five ganglia separated by long connectives - 0.

Diphyllostomatidae

No literature available.

No fresh specimens were dissected.

Glaphyridae

No literature available.

No fresh specimens were dissected.

Trogidae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 5.5)

Suboesophageal ganglion - situated on the margin of the head and thorax; separated from the prothoracic ganglion by long connectives. Mesothoracic ganglion - separated from the prothoracic ganglion by long connectives, but separated from the metathoracic ganglion by short, but still clearly visible connectives. Short connectives visible between the metathoracic and first abdominal ganglion. Six abdominal ganglia - clearly visible but the connectives only distinguishable as small holes between the different ganglia (e.g. *Polynoncus pedestris* (Fig. 5.5)).

PHYLOGENETIC INTERPRETATION

(CH6) Suboesophageal ganglion situated ventrally against the foregut - 0;

(CH7) all three thoracic ganglia visible - 0;

(CH8) abdominal ganglia separately visible but connectives absent - only distinction between

ganglia is small holes between the ganglia and first abdominal ganglia fused to the metathoracic ganglion - 1.

Bolboceratidae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 5.6)

Suboesophageal ganglion - situated on the margin between head and thorax (e.g. *Bolbocaffer* sp. (Fig. 5.6)) suboesophageal ganglion - separated from prothoracic ganglion by long connectives. Meso- and metathoracic ganglia - separated by short, visible connectives. Abdominal ganglia - fused to each other and to metathoracic ganglion. Different abdominal ganglia - separated by holes (left by the shortening of the connectives).

PHYLOGENETIC INTERPRETATION

(CH6) Suboesophageal ganglion situated ventrally against the foregut - 0;

(CH7) all three thoracic ganglia visible - 0;

(CH8) first abdominal ganglion fused to metathoracic ganglia, all abdominal ganglia fused - 2.

Pleocomidae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 5.7)

Suboesophageal ganglion - situated on the margin of the head and thorax and separated from the prothoracic ganglion by long connectives. Mesothoracic ganglion - separated from the prothoracic ganglion by long connectives. Very short connectives separate the meso- and metathoracic ganglia. First abdominal ganglion - situated close to the metathoracic ganglion; separated from it by short connectives. The following five abdominal ganglia - separated from one another by long connectives. Fifth and sixth ganglia - situated in the abdomen (e.g. *Pleocoma simbriata* (Fig. 5.7)).

PHYLOGENETIC INTERPRETATION

(CH6) Suboesophageal ganglion situated ventrally against the foregut - 0;

(CH7) all three thoracic ganglia visible - 0;

(CH8) first abdominal ganglion fused to metathoracic ganglion, last five ganglia separated by

long connectives - 0.

Geotrupidae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG.5.8; 5.9)

Suboesophageal ganglion - situated on the margin of the head and thorax; separated from the prothoracic ganglion by long connectives (Fig. 5.8; 5.9). Meso- and metathoracic ganglia - separated by short connectives (e.g. *Taurocerastes* sp. (Fig. 5.8)). Meso- and metathoracic ganglia of the Geotrupinae - separated only by small holes (e.g. Geotrupidae sp. (Fig. 5.9)). Abdominal ganglia - all fused to each other. Small holes - separate individual ganglia. First abdominal ganglion - fused to the metathoracic ganglion.

PHYLOGENETIC INTERPRETATION

(CH6) Suboesophageal ganglion situated ventrally against the foregut - 0;

(CH7) all three ganglia visible - 0; Prothoracic ganglion is visible, meso- and metathoracic ganglia fused - 1;

(CH8) all abdominal ganglia fused to each other and to the metathoracic ganglion - 2.

Ochodaeidae

No literature available.

No fresh specimens were dissected.

Ceratocanthidae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 5.10)

Suboesophageal ganglion - situated on the margin of the head and thorax; separated from the prothoracic ganglion by short connectives. Meso- and metathoracic ganglia - separated from each other by very short connectives. Abdominal ganglia - all fused to each other and to the metathoracic ganglion (e.g. Ceratocanthidae sp. (Fig. 5.10)).

PHYLOGENETIC INTERPRETATION

(CH6) Suboesophageal ganglion situated ventrally against the foregut - 0;

(CH7) all three ganglia are visible - 0;

(CH8) abdominal ganglia fused to each other and to the metathoracic ganglion - 2.

Hybosoridae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 5.11)

Suboesophageal ganglion - situated on the margin of the head and thorax; separated from the prothoracic ganglion by long connectives. Meso- and metathoracic ganglia - separated from each other by short connectives. First abdominal ganglion - separated from the metathoracic ganglion by short connectives. First three abdominal ganglia - clearly visible. Last ganglionic mass consists of abdominal ganglia four, five and six (e.g. *Hybosorus illigeri* (Fig. 5.11)).

PHYLOGENETIC INTERPRETATION

(CH6) Suboesophageal ganglion situated ventrally against the foregut - 0;

(CH7) all three ganglia are visible - 0;

(CH8) first three abdominal ganglia separate, ganglia four to six fused – 1.

Scarabaeidae: Aphodiinae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 5.12)

Suboesophageal ganglion - situated on the margin of the head and thorax; separated from the prothoracic ganglion by rather long connectives. Meso- and metathoracic ganglia - separated from each other by very short connectives. All abdominal ganglia - fused to each other and to the metathoracic ganglion (e.g. *Aphodius russatus* (Fig. 5.12)).

PHYLOGENETIC INTERPRETATION

(CH6) Suboesophageal ganglion situated ventrally against the foregut - 0;

(CH7) all three ganglia are visible - 0;

(CH8) abdominal ganglia fused to each other and to the metathoracic ganglion – 2.

Scarabaeidae: Scarabaeinae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 5.13)

Suboesophageal ganglion - situated on the margin of the head and the thorax; next to the foregut; separated from the prothoracic ganglion by long connectives. Pro- and mesothoracic ganglion - separated by very short connectives. Meso- and metathoracic ganglia - completely fused. All abdominal ganglia - fused to each other and to the metathoracic ganglion forming a compact mass (e.g. *Onitis caffer* (Fig. 5.13)).

PHYLOGENETIC INTERPRETATION

(CH6) Suboesophageal ganglion situated ventrally against foregut - 0;

(CH7) prothoracic ganglion visible, meso- and metathoracic ganglia fused - 1;

(CH8) all abdominal ganglia fused to each other and to metathoracic ganglion - 2.

Scarabaeidae: Melolonthinae

LITERATURE REVIEW

Menees (1961) described the morphology of the ventral nervous system in *Amphimallon majalis*. The suboesophageal and prothoracic ganglion are separate, while the meso- meta- and, all abdominal ganglia are fused, forming a compact mass.

The nervous system of *Phyllophaga anxia* is described by Berberet & Helms (1972). The suboesophageal ganglion is separated from the prothoracic ganglionic mass by short connectives. The prothoracic ganglionic mass consists of the pro- meso and meta- as well as all abdominal ganglia, fused together.

MORPHOLOGICAL DESCRIPTION (FIG. 5.14 A - C)

Suboesophageal ganglion - moved posteriorly and connected to the brain by means of long connectives (Fig. 5.14 A; B); or - anterior; connected with short connectives to brain (Fig, 5.14 C). Alimentary canal - travels from mouth (situated dorsally) to ventral position between the connectives. Suboesophageal ganglion as well as the three thoracic ganglia - all connected to each other by very short connectives (Fig, 5.14 A); sometimes only visible as small holes. Suboesophageal ganglion - connected to prothoracic ganglion with short connectives (Fig. 5.14 B; C). Prothoracic ganglion - united to mesothoracic ganglion (Fig. 5.14 A; C); connected to mesothoracic ganglion by short connectives (Fig. 5.14 B). Meso- and metathoracic ganglia - always fused. Abdominal ganglia - always fused to each other and to the metathoracic ganglion.

PHYLOGENETIC INTERPRETATION

(CH6) Suboesophageal ganglion - situated anteriorly against alimentary canal - 0; moved posteriorly - 1;

(CH7) prothoracic ganglion is visible, meso- and metathoracic ganglia fused - 1;

(CH8) all abdominal ganglia fused to each other and to the metathoracic ganglion - 2.

Scarabaeidae: Rutelinae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 5.15)

Suboesophageal ganglion of the *Anomala* sp. and *Callodes frenchi* (Fig. 5.15*)* - moved posteriorly; connected to the brain by long connectives. Pharynx (in these species) - therefore does not lie in close proximity to the suboesophageal ganglion. Prothoracic ganglion - separated from the suboesophageal ganglion by long connectives. Prothoracic ganglion - separated from the mesothoracic ganglion by very short connectives. Meso- and metathoracic ganglia - fused to each other. A small hole visible between meso- and metathoracic ganglia. Abdominal ganglia - all fused to each other and to the metathoracic ganglion.

In two Rutelinae species - suboesophageal ganglion moved posteriorly and connected to the prothoracic ganglion by very short connectives. In *Leptohoplia testaceipennis* and two Rutelinae species from Plettenberg Bay and Pretoria - suboesophageal ganglion situated on the margin of the head and thorax.

PHYLOGENETIC INTERPRETATION

(CH6) Suboesophageal ganglion either situated on the margin of the head and thorax - 0 or moved posteriorly - 1;

(CH7) prothoracic ganglion is visible, meso- and metathoracic ganglia fused - 1;

(CH8) all abdominal ganglia fused to each other and to the metathoracic ganglion – 2.

Scarabaeidae: Hopliinae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 5.16)

Suboesophageal ganglion - situated on the margin of the head and thorax and separated from the prothoracic ganglion by short connectives. Pro- and mesothoracic ganglia - separated by long connectives. Meso- and metathoracic ganglia - fused, with only small holes where the connectives once were present. All abdominal ganglia - fused to each other and to the metathoracic ganglion (Fig. 5.16).

PHYLOGENETIC INTERPRETATION

(CH6) Suboesophageal ganglion is situated on the margin of the head and thorax - 0;

(CH7) prothoracic ganglion is visible, meso- and metathoracic ganglia fused - 1;

(CH8) all abdominal ganglia fused to each other and to the metathoracic ganglion - 2.

Scarabaeidae: Dynastinae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 5.17)

Oesophagial ganglion - moved slightly to the posterior (not situated on the margin of the head and thorax); not as far posterior as is found in some Melolonthinae species; separated from the prothoracic ganglion by connectives of medium length. Meso- meta and abdominal ganglia - all fused together, no connectives are visible (Fig. 5.17).

PHYLOGENETIC INTERPRETATION

(CH6) Suboesophageal ganglion is situated slightly posterior of the margin between the head and thorax - 1;

(CH7) prothoracic ganglion is visible, meso- and metathoracic ganglia fused - 1;

(CH8) all abdominal ganglia fused to each other and to the metathoracic ganglion - 2.

Scarabaeidae: Cetoniinae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 5.18)

Suboesophageal ganglion - situated on the margin of the head and the thorax; separated from the prothoracic ganglion by short connectives. Prothoracic ganglion - separated from the mesothoracic ganglion by short connectives. Meso- metathoracic ganglia - fused to abdominal ganglia. Meso- and metathoracic ganglia - distinguishable from each other by a

small hole - representing the shortening of connectives (Fig. 5.18).

PHYLOGENETIC INTERPRETATION

(CH6) Suboesophageal ganglion is situated on the margin of the head and thorax - 0;

(CH7) prothoracic ganglion is visible, meso- and metathoracic ganglia fused - 1;

(CH8) all abdominal ganglia fused to each other and to the metathoracic ganglion - 2.

Scarabaeidae: Trichiinae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 5.19)

Suboesophageal ganglion - situated on the margin of the head and thorax; separated from the prothoracic ganglion by short connectives. Meso- and metathoracic ganglia – fused; a small hole visible between the two ganglia. Abdominal ganglia - all fused to each other and to the metathoracic ganglion (e.g. *Campulipus limbatus* (Fig. 5.19)).

PHYLOGENETIC INTERPRETATION

(CH6) Suboesophageal ganglion is situated on the margin of the head and thorax - 0;

(CH7) prothoracic ganglion is visible, meso- and metathoracic ganglia fused - 1;

(CH8) all abdominal ganglia fused to each other and to the metathoracic ganglion - 2.

Scarabaeidae: Valginae, Oncerinae, Chasmatopterinae and Orphninae

No literature available.

No fresh specimens were dissected.

PLATE 10

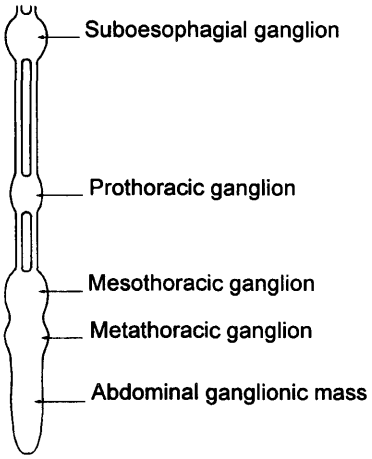


Fig. 5.1

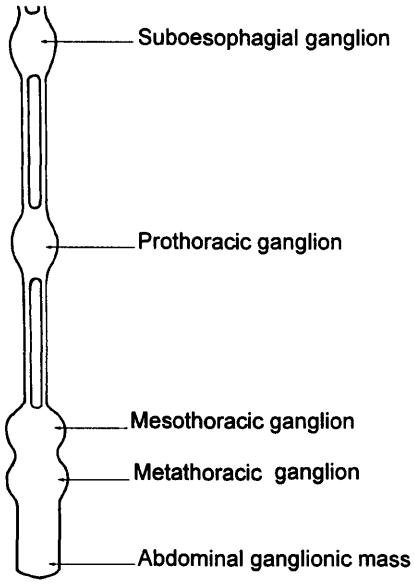


Fig. 5.2

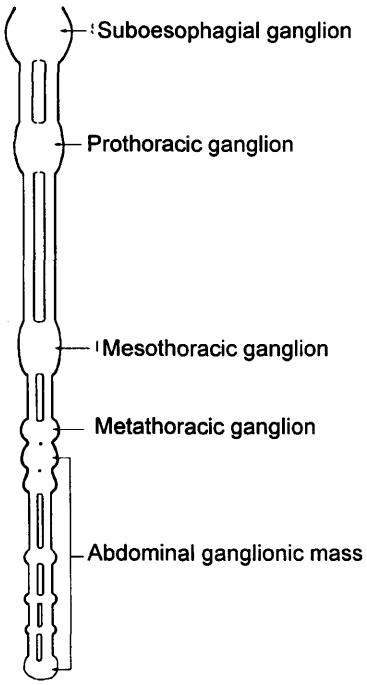


Fig. 5.3

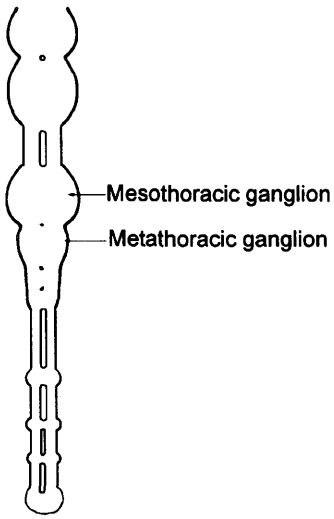


Fig. 5.4

Fig. 5.1 Nervous system of a *Glaresis* species (Glaresidae)
Fig. 5.2 Nervous system of *Odontotaenius disjunctus* (Passalidae)
Fig. 5.3 Nervous system of a *Figulus* species (Lucanidae)
Fig. 5.4 Nervous system of *Syndesus comutus* (Lucanidae)
Drawings not to scale

PLATE 11

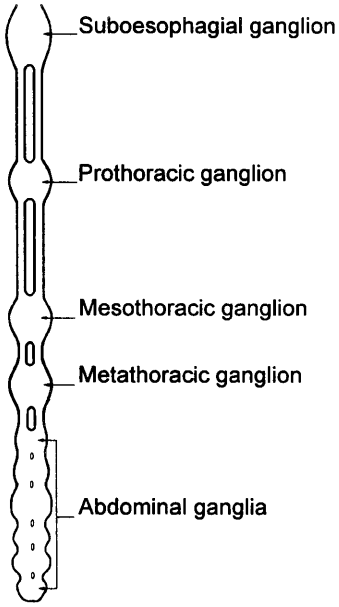


Fig. 5.5

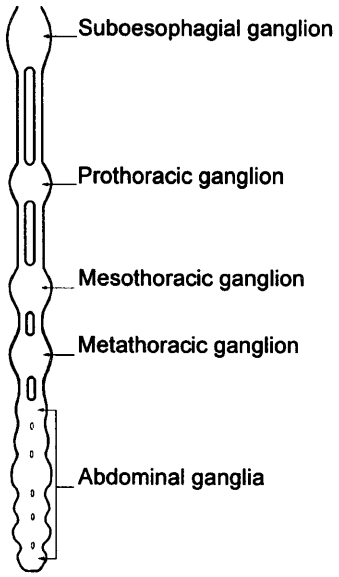


Fig. 5.6

Fig. 5.7

Fig. 5.8

Fig. 5.9

Fig. 5.5 Nervous system of *Polynoncus pedestris* (Trogidae)
Fig. 5.6 Nervous system of a *Bolbocaffer* species (Bolboceratidae)
Fig. 5.7 Nervous system of *Pleocoma simbriata* (Pleocomidae)
Fig. 5.8 Nervous system of a *Taurocerastes* species (Geotrupidae)
Fig. 5.9 Nervous system of *Geotrupes spiniger* (Geotrupidae)
Drawings not to scale

PLATE 12

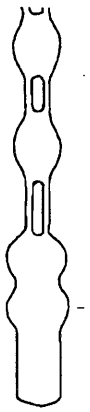


Fig. 5.10

Fig. 5.11

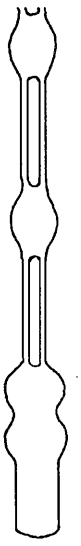


Fig. 5.12

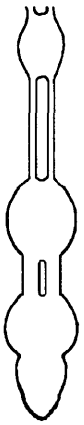


Fig. 5.13

Fig. 5.10 Nervous system of a Ceratocanthidae species
Fig. 5.11 Nervous system of *Hybosorus illigeri* (Hybosoridae)
Fig. 5.12 Nervous system of *Aphodius russatus* (Aphodiinae)
Fig. 5.13 Nervous system of *Onitis caffer* (Scarabaeinae)
Drawings not to scale

PLATE 13

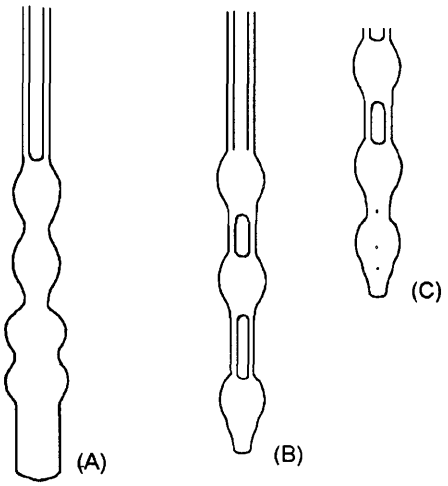


Fig. 5.14

Fig. 5.15

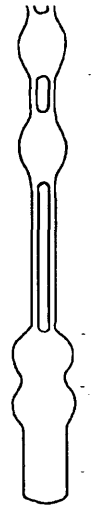


Fig. 5.16

Fig. 5.17

Fig. 5.14 Nervous system differences in Melolonthinae
Fig. 5.15 Nervous system of a typical Rutelinae species
Fig. 5.16 Nervous system of a typical Hopliinae species
Fig. 5.17 Nervous system of a typical Dynastinae species
Drawings not to scale

PLATE 14

Fig. 5.18

Fig. 5.19

Fig. 5.18 Nervous system of a typical Cetoniinae species
Fig. 5.19 Nervous system of *Campulipus limbatus* (Trichiinae)
Drawings not to scale

6. INTERNAL FEMALE REPRODUCTIVE ORGANS

Introduction

The general structure and morphology of the internal female reproductive organs were discussed in Chapter 3. Characters as well as the polarity of character states were also determined in Chapter 3. In this chapter, literature (if available) pertaining to individual families, and in the case of Scarabaeidae, subfamilies, are discussed. Morphological descriptions (of species dissected from each taxon - species dissected listed in Appendix 1.1) as well as phylogenetic interpretation of each of the identified characters, follow.

The aims of this chapter are to discuss:

- relevant literature dealing with the morphology of the internal female reproductive organs of each taxon of the Scarabaeoidea
- the morphology of the internal female reproductive organs of each taxon (results from the research done for the thesis)
- phylogenetic trends in the morphology of the internal female reproductive organs for each taxon

Glaresidae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 6.1)

Six ovarioles per side (e.g. *Glaresis* sp. (Fig. 6.1)). Bursa copulatrix - elongated and membranous. Spermatheca - rounded and membranous. Spermathecal accessory gland - elongated and membranous. Spermathecal duct - short and basally attached. Accessory glands - absent. Vagina - membranous.

PHYLOGENETIC INTERPRETATION

(CH9) Two ovaries per female - 0;

CH10) six ovaries per side - 0;

(CH11) bursa copulatrix lengthened - 0;

(CH12) glandular structures absent form female reproductive tract - 0;

(CH13) spermathecal duct basally attached - 0.

Passalidae

LITERATURE REVIEW

Each ovary of the female genitalia of *Odontotaenius disjunctus* possesses two ovarioles (Williams, 1945). The bursa copulatrix is a short sac, while the spermathecal duct is rather short and thick.

The paired ovaries of *Passalus cornutus* are elongated, tapering structures (Krause, 1946). The ovarioles unite at their bases to form two lateral oviducti, which are joined to form a median oviduct. The bursa copulatrix is an elongated sac-like structure. The bursa receives the spermathecal duct that is rather short, bearing a prominent spermatheca and gland.

DESCRIPTION (FIG. 6.2)

Two ovarioles per side. Bursa - elongated and muscular. Spermatheca - strongly membranous and elongated. Spermathecal accessory gland - membranous and elongated. Spermathecal duct - moderately long and basally attached. No accessory glands are present. The vagina is muscular (e.g. *O. disjunctus* (Fig. 6.2)).

PHYLOGENETIC INTERPRETATION

(CH9) Two ovaries per female – 0;

(CH10) two ovarioles per side - 1

(CH11) bursa copulatrix lengthened - 0;

(CH12) glandular structures absent from female reproductive tract - 0;

(CH13) spermathecal duct attached basally - 0.

Lucanidae

LITERATURE REVIEW

Holloway (1960) investigated the taxonomy and phylogeny of the Lucanidae and studied, amongst other characters, the female internal genitalia. She described and illustrated them and found that the bursa was elongated and usually distinctive, the spermathecal duct varied from short to long and wide and that the spermatheca had different distinct forms, varying from round and sclerotised to duct-like or bulbous. She examined: *Dendroblax earlii*, *Lamprima latreillei*, *Streptocerus speciosus*, *Dorcus parallelipipedus*, *Colophon cameroni*, *Pholidotus humboldti*, *Ryssonotus politus*, *Ryssonotus nebulosus*, *Figulus regularis*, *Ceratognathus parrianus*, and *Ceruchus chrysomelinus.*

Ritcher & Baker (1974) investigated the number of ovarioles in the Lucanidae. Ovariole number 6-6 was found in Platycerinae and Aesalinae, while an ovariole number of 12-12 was observed in one species each of Sinodendroninae and Lucaninae. Robertson (1961) cited Stein (1847) as finding 12-12 ovarioles in *D. parallelipipedus* (Dorcinae).

DESCRIPTION (FIG. 6.3, 6.4; 6.5; 6.6)

Six ovarioles per side - present in *Platyceropsis* sp., *Figulus* sp. and *Syndesus cornutus* (Fig. 6.3). Twelve ovarioles per side - present in *Prosopocoilus natalensis* and *Sinodendron rugosum*. Bursa copulatrix - lengthened (in all species). Bursa - membranous in all species studied except *Ceratognathus* sp. (Fig. 6.4) where it is muscular. Spermatheca - round (e.g. *Ceratognathus* sp. (Fig. 6.4)), fingershaped (e.g. *Rhyssonotus nebulosus* (Fig. 6.5)) and elongated - in all other species (e.g. *Sinodendron cylindricum* (Fig 6.6)). Spermatheca - membranous (all species). Spermathecal accessory gland - varies from round (e.g. *Ceratognathus* sp. (Fig. 6.4)) to elongated (e.g. *Cacostomus squamosus* and *S. cylindricum* (Fig. 6.6)). Spermathecal duct - moderate to long; thin (e.g. *Ceratognathus* (Fig. 6.4)) to thick (e.g. *R. nebulosus* (Fig. 6.5)) and basally attached. Accessory glands - not present. Vagina - membranous (e.g. *S. cylindricum*) all species - except in *P. natalensis*, vagina - muscular.

PHYLOGENETIC INTERPRETATION

(CH9) Two ovaries per female – 0;

(CH10) six ovarioles per side (*Platyceropsis sp., Figulus sp., S. cornutus*) - 0,

twelve ovarioles per side (*P. natalensis*, *S. rugosum*) - (unordered character state) - 1;

(CH11) bursa copulatrix lengthened - 0;

(CH12) glandular structures absent form female reproductive tract - 0;

(CH13) spermathecal duct basally attached - 0.

Diphyllostomatidae

LITERATURE REVIEW

Holloway (1972) described part of the internal female genitalia of *Diphyllostoma linsleyi*. The female possesses a broad, cylindrical and dilated bursa copulatrix. The spermatheca is inconspicuous with a small, stalked accessory gland. The spermathecal duct is of medium length and rather thick. No accessory glands are present.

DESCRIPTION

No females were dissected.

PHYLOGENETIC INTERPRETATION (ACCORDING TO HOLLOWAY, 1972)

(CH9) Two ovaries per female – 0;

(CH10) number of ovarioles per side - 9 (missing data);

(CH11) bursa copulatrix lengthened - 0;

(CH12) glandular structures absent form female reproductive tract - 0;

(CH13) spermathecal duct attached basally - 0.

Glaphyridae

LITERATURE REVIEW

Females of *Lichnanthe rathvoni* were examined by Ritcher & Baker (1974). They found an ovariole number of 6-6 per ovary.

DESCRIPTION (FIG. 6.7)

Bursa copulatrix, spermatheca and spermathecal accessory gland - elongated and membranous. Spermathecal duct - moderately long and basally attached (e.g. *Lichnanthe apina* (Fig. 6.7). Accessory glands - absent. Vagina - membranous.

PHYLOGENETIC INTERPRETATION

(CH9) Two ovaries per female - 0;

(CH10) six ovarioles per side - 0;

(CH11) bursa copulatrix lengthened - 0;

(CH12) glandular structures absent form female reproductive tract - 0;

(CH13) spermathecal duct basally attached - 0.

Trogidae

LITERATURE REVIEW

Ritcher & Baker (1974) indicated that the ovariole numbers of the different genera differ. *Omorgus* (specimens from Texas, New Mexico and Arizona) possess 3-3 ovariole number, while the ovariole number present in *Trox* is 6-6 (specimens from Oregon, Texas, New Mexico and Arizona).

DESCRIPTION (FIG. 6.8; 6.9; 6.10; 6.11)

Six ovarioles - present in both southern Africa genera (e.g. *Trox squamiger* (Fig. 6.8) and *Omorgus asperulatus* (Fig. 6.9)). Bursa copulatrix - either elongated (all *Trox* and *Polynoncus* species) (e.g. *T. squamiger* (Fig. 6.8)) or U-shaped - the ventral, distal wall of

bursa joined to ventral body wall (all *Omorgus* sp.) (e.g. *O. asperulatus* (Fig. 6.9)). Bursa - membranous (all *Polynoncus* sp. and *Omorgus* sp.) to muscular (all *Trox* sp.). Spermatheca - round (all *Omorgus* sp.) (e.g. *Omorgus suberosus* (Fig. 6.10) to elongate (all *Trox* and *Polynoncus* sp.) (e.g. *Trox rhyparoides* (Fig. 6.11)). Spermatheca - membranous. Spermathecal duct - moderately long and basally attached. No accessory glands are present. Vagina - membranous (e.g. *Polynoncus longitarsis*) or muscular (e.g. *Trox sulcatus*).

PHYLOGENETIC INTERPRETATION

(CH9) Two ovaries per female - 0;

(CH10) six ovarioles per side (southern African genera) - 0; three ovarioles per side (North American *Omorgus* species - Ritcher & Baker, 1977) -1;

(CH11) bursa copulatrix lengthened (*Trox* sp. and *Polynoncus* sp.) - 0, anterior wall of bursa copulatrix connected to the ventral body wall (*Omorgus* sp.) - 1;

(CH12) glandular structures absent from female reproductive tract - 0;

(CH13) spermathecal duct basally attached - 0.

Bolboceratidae

LITERATURE REVIEW

Williams (1945) studied two species belonging to this family, *Bolbocerosoma farctum* and *Eucanthus lazarus.* Females of *B. farctum* possess two ovaries each consisting of one ovariole. An elongated bursa and spermatheca are present. The female genitalia structure of *E. lazarus* is similar to that of *B. farctum*.

Three species of this taxon (*Bolboceras obesum*, *Bolborhombus carinatus* and *E. lazarus*) possess a 6-6 ovariole number (Ritcher & Baker, 1974).

DESCRIPTION (FIG. 6.12; 6.13)

Six ovarioles per side. Bursa copulatrix - flattened and membranous (e.g. *Bolbolaeus truncatus* (Fig. 6.12)); elongated (e.g. *Bolbocerus obesus* (Fig. 6.13)). Spermatheca and spermathecal accessory gland - elongated and membranous. Spermathecal duct - moderate in length, thin; varies from basally attached (*B. obesus* and *Elephastomus meraldus*) to more distally attached (*B. truncatus)*. Accessory glands - absent (*E. meraldus* and *Bolbocaffer* sp.); present (*B. truncatus*) (This is the first taxon where a flattened bursa occurs- present in six of the seven studied species; absent in *B. obesus*). Vagina - membranous.

PHYLOGENETIC INTERPRETATION

(CH9) Two ovaries per female - 0;

(CH10) six ovarioles per side - 0;

(CH11) bursa copulatrix lengthened - 0 to flattened - 1;

(CH12) glandular structures absent form female reproductive tract - 0 to present - 1;

(CH13) spermathecal duct basally attached - 0 to distally attached - 1.

Pleocomidae

LITERATURE REVIEW

Ritcher & Baker (1974) examined seven species belonging to *Pleocoma* and found the ovariole number varying from 14-25 ovarioles in each ovary.

DESCRIPTION (FIG. 6.14)

No fresh or alcohol preserved females were dissected but from the dried specimens, the following descriptions can be made. Bursa copulatrix, spermatheca and spermathecal accessory gland - elongated and membranous (e.g. *Pleocoma edwardsii* (Fig. 6.14)). Spermathecal duct - moderately long, thin and basally attached. Accessory glands - absent. Vagina - muscular.

PHYLOGENETIC INTERPRETATION

(CH9) Two ovaries per female - 0;

(CH10) between 14 and 25 ovarioles per side - 1;

(CH11) bursa copulatrix lengthened - 0;

(CH13) glandular structures absent form female reproductive tract - 0;

(CH14) spermathecal duct basally attached - 0.

Geotrupidae

LITERATURE REVIEW

Ritcher & Baker (1974) found a 6-6 ovariole number for all species studied belonging to the Geotrupidae. Halffter & Lopez-Guerrero (1985) studied some species belonging to *Geotrupes* and found two ovaries and 6-6 ovariole number. A pear-shaped spermatheca and a short duct are present.

Bovo & Zunino (1983) described four new genera (*Sinogeotrupes*, *Chromogeotrupes*, *Eogeotrupes* and *Epigeotrupes*) on the basis of male and female genital features.

Exodermal female structures (bursa, spermatheca and gland as well as the ovipositor) and external male sclerotised structures were used to describe the genera. The structure and form of the spermatheca and spermathecal duct were compared between species. The spermatheca appears elongated to pear-shaped in all four species, while the spermathecal gland is either elongated and with a very slight bulbous tip, or the tip rounded to look likea ball. The bursa copulatrix is either small and slightly elongated (found in *Sinogeotrupes subseriatellus*) or larger and flattened (*Geotrupes stercorarius*).

Zunino (1984) based systematic research (according to cladistic criteria) on the structure of the male and female reproductive organs. He investigated the internal female reproductive organs of the species belonging to 23 genera of the Geotrupinae. The systematic importance of these characters were stressed, particularly at genus and subfamily level. On the basis of phylogenetic analysis as well as available paleontologic and ecological data, certain assumptions about the origin of the family was made.

DESCRIPTION (FIG. 6.15 – 6.18)

Six ovarioles per side. Bursa copulatrix - either elongated or flattened. Elongated - *Enoplutrupes bieti* (Fig. 6.15), *Lethrus apterus* (Fig. 6.16), *Geotrupes splendidus* and *Geotrupes gautemalensis.* Flattened - *Mycotrupes gagei* (Fig. 6.17, 6.18), *Frickius variolosus* and *Taurocerastes* sp. Bursa copulatrix - varies from membranous to muscular. Muscular – *E. bieti* (Fig. 6.18) and *Frickius variolosus*. Spermatheca and spermathecal accessory gland - elongated and membranous. Spermathecal duct - moderately long; basally attached. Accessory glands - vary from absent – *Lethrus apterus* (Fig. 6.16) to present (*Mycotrupes gagei* (Fig. 6.17)). Vagina - membranous to muscular (muscular in *F. variolosus and Taurocerastes* sp.).

PHYLOGENETIC INTERPRETATION

(CH9) Two ovaries per female - 0;

(CH10) six ovarioles per side - 0;

(CH11) bursa copulatrix lengthened - 0 to flattened - 1;

(CH12) glandular structures absent form female reproductive tract - 0 to present - 1;

(CH13) spermathecal duct basally attached - 0.

Ochodaeidae

LITERATURE REVIEW

Carlson & Ritcher (1974) found a 6-6 ovariole number in *Ochodaeus* and *Pseudochodaeus*.

DESCRIPTION (FIG. 6.19)

Bursa copulatrix, spermatheca and spermathecal accessory gland - elongated and muscular. Spermathecal duct moderately long and distally attached. Accessory glands - absent. Vagina - membranous (e.g. *Ochodaeus inarmatus* (Fig. 6.19)).

PHYLOGENETIC INTERPRETATION

(CH9) Two ovaries per female - 0;

(CH10) six ovarioles per side - 0

(CH11) bursa copulatrix lengthened - 0;

(CH12) glandular structures absent from female reproductive tract - 0;

(CH13) spermathecal duct distally attached - 1.

Ceratocanthidae

LITERATURE REVIEW

A *Cloeotus* species examined by Ritcher & Baker (1974) possessed an ovariole number of 6-6.

DESCRIPTION (FIG. 6.20)

Six ovarioles per side - present. Bursa copulatrix, spermatheca and spermathecal accessory glands - elongated and membranous. Spermathecal duct - moderately long; basally attached. Accessory glands - absent. Vagina - membranous (e.g. Ceratocanthidae sp. (Fig. 6.20)).

PHYLOGENETIC INTERPRETATION

(CH9) Two ovaries per female - 0;

(CH10) six ovarioles per side - 0;

(CH11) bursa copulatrix lengthened - 0;

(CH13) glandular structures absent from female reproductive tract - 0;

(CH13) spermathecal duct basally attached - 0.

Hybosoridae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 6.21)

Six ovarioles per side. Bursa copulatrix - elongated; varies from membranous to muscular (only *Phaeochrous mashunus*). Spermatheca and spermathecal accessory gland - elongated and membranous. Spermathecal duct - short in *P. mashunus* to moderately long (*Hybosorus illigeri*); basally attached. Accessory glands - absent. Vagina varies from membranous (e.g. *Anaides* sp. (Fig. 6.21)) to muscular (*P. mashunus*).

PHYLOGENETIC INTERPRETATION

(CH9) Two ovaries per female - 0;

(CH10) six ovarioles per side - 0;

(CH11) bursa copulatrix lengthened - 0;

(CH12) glandular structures absent from female reproductive tract - 0;

(CH13) spermathecal duct basally attached - 0.

Scarabaeidae: Aphodiinae

LITERATURE REVIEW

A range of ovariole numbers has been found in this taxon. The tribe Aphodiini possesses species with 5-5, 6-6 and 7-7 ovariole numbers. Aegialiini and Eupariini possess 3-3 ovariole numbers, while ovariole numbers of 2-2 and 3-3 are present in Psammodiini (Ritcher & Baker, 1974).

DESCRIPTION (FIG. 6.22; 6.23)

Six ovarioles per side - present. Bursa copulatrix - elongated in *Aphodius tasmaniae* (Fig. 6.22), *Aetaenius cognatus*, *Aphodius bimentarius* and *Aphodius fossor*. Rest of the species studied - bursa copulatrix - flattened (appearing much the same as that of the Scarabaeinae - e.g. *Aphodius russatus* (Fig. 6.23)). Bursa - varies from membranous (e.g. *A. cognatus*) to slightly muscular (e.g. *A. tasmaniae*). Spermatheca and spermathecal accessory gland - elongated and membranous. Spermathecal duct - varies from moderately long (e.g. *A. cognatus*) to very long (e.g. *A. fossor*). Attachment - varies from basally attached (e.g. *A. tasmaniae*) to distally attached (e.g. *A. fossor*). Accessory glands - absent. Vagina - membranous.

PHYLOGENETIC INTERPRETATION

(CH9) Number of ovaries - two ovaries per female - 0;

(CH10) six ovarioles per side in Aphodiini (unordered character state) - 0; two ovarioles per side in some Psammodiini (Ritcher & Baker, 1974); three ovarioles per side in Aegialiini and Eupariini and some species of Psammodiini (Ritcher & Baker, 1974) - 1;

(CH11) bursa copulatrix lengthened - 0 as well as flattened in some species - 1;

(CH12) glandular structures absent from female reproductive tract - 0;

(CH13) spermathecal duct is basally attached in some species - 0, but in other distally attached - 1.

Scarabaeidae: Scarabaeinae

LITERATURE REVIEW

The female reproductive system includes a median oviduct, flattened bursa, vagina, spermatheca with duct and associated gland and ovary. The most striking feature of the female system is that it possesses a single ovary (Heymons, 1930) - on the left side. Pluot (1979), however, found that females of *Onthophagus lecontei* possess one left ovary consisting of two ovarioles.

The following authors also described the presence of only one ovary with one ovariole:

- Heymons (1929 and 1930) studied species belonging to *Scarabaeus*, *Sisyphus*, *Canthon Pinotus* and *Copris*. All species possess a flattened bursa and only one ovary with one ovariole. Females of *Scarabaeus sacer*, however, were found to possess one ovary with two ovarioles on the left side.
- In *Pinotus carolinus* (Williams, 1945) the spermatheca is C-shaped and chitinous and connected to the bursa with a medium length duct. The bursa is flattened. One ovary with one ovariole is also present.
- Robertson (1961) - *Scarabaeus sacer*, *Scarabaeus semipunctatus*, *Scarabaeus variolosus* and *Scarabaeus laticollis*.
- Halffter & Matthews (1966) –species of *Scarabaeus*, *Canthon*, *Copris*, *Dichotomius* and *Onthophagus*.
- Ritcher & Baker (1974) – one ovary for the members of the Scarabaeinae they studied (present on the left side).

- Srivastava (1951) - *Onitis distinctus*
- Edmonds (1974) - *Coprophanaeus lancifer*
- Dajoz (1972) – *S. semipunctatus.*
- Halffter & Lopez (1977) – *Phanaeus* sp. This genus possesses only one ovariole and the authors refer to the bursa (that is flattened in the Scarabaeinae) as the vagina. The spermatheca is a sclerotised, U-shaped seminal receptacle, possessing a spermathecal accessory gland. The spermathecal duct is long.
- The reduction of the female system has also been observed by authors like Halffter et al. 1982; Halffter & Lopez 1977; Halffter & Matthews, 1966; Tyndale-Biscoe & Watson, 1977; Tyndale-Biscoe, 1978; Halffter & Edmonds, 1982.

DESCRIPTION (FIG. 6.24 – 6.28)

Only one ovariole -present (e.g. *Onthophagus gazella* (Fig. 6.24)) (this species is sometimes referred to as *Digitonthophagus gazella* (Hanski & Cambefort, 1991)); with exception - Pinotini (Fig. 6.25) where the remains of a second ovariole are still visible. This second ovariole - very reduced; does not appear to be functional. Bursa copulatrix - elongated (only in *Temnoplectron rotundum (*Fig. 6.26)) flattened (in all other species studied). Bursa copulatrix - varies from membranous (only in *T. rotundum*) to muscular. Spermatheca - elongated and sclerotised. Spermathecal accessory gland - slightly roundish (e.g. *Labroma umbratilis* (Fig. 6.27)) to elongated (e.g. *Epirinus validus*) and membranous. Spermathecal duct - moderately long (e.g. *Euoniticellus intermedius*) to very long (e.g. *Sisyphus* sp.). Attachment varies from - basally attached (e.g. *E. validus*, *Scarabaeus flavicornis*, *Onitis alexis*, *E. intermedius*, *Metacatharsius* sp., *Cephalodesmius armiger*, *Sisyphus* sp. and all four Coprini sp.) to distally attached (e.g. *Onitis fulgidus*). (Attachment of the spermathecal duct, structure of the vaginal wall as well as the presence or absence of accessory glands varies even between species in a tribe).

Accessory glands - absent (e.g. *E. validus*, *Metacatharsius* sp., *Phanaeus daman*, *Eurysternus magnus*, *T. rotundum*, *O. gazella*, *Phalops* sp.1 *Sisyphus* sp.1, *O. fulgidus*) to present (all other species studied - e.g. *Copris* sp. (Fig. 6.28)) Accessory glands - opening next to the bursa copulatrix. Vagina - membranous (e.g. *T. rotundum*) to muscular (e.g. *Diastellopalpus thomsoni*).

PHYLOGENETIC INTERPRETATION

(CH9) one ovary and reduced second one per female 1; - 1 ovary per female - 2;

(CH10) less than six ovarioles per side - 1;

(CH11) bursa copulatrix lengthened - 0 (only in *T. rotundum*) to flattened - 2;

(CH12) glandular structures **absent** - 0 (*E. validus*, *Metacatharsius* sp., *P. daman*, *E. magnus*, *T. rotundum*, *O. gazella*, *Phalops* sp., *Sisyphus* sp., *O. fulgidus*)

present (*Anachalcos convexus*, *S. flavicornis*, *O. alexis*, *E. intermedius*, *C. armiger*, *Diastellopalpus thomsoni*, *Labroma umbratilis*, *Onthophagus* sp., *Proagoderus fossidorsis*, *Pachylomerus femoralis*, *Circellium bacchus*, *Copris* sp., 1 *Copris* sp. 2) - 1;

(CH13) spermathecal duct attachment varies from **basally attached** (*E. validus*, *S. flavicornis*, *O. alexis*, *E. intermedius*, *Metacatharsius* sp. 1, *C. armiger*, *Sisyphus* sp. 1, all four Coprini sp.) - 0;

distally attached (*A. convexus*, *T. rotundum*, *D. thomsoni*, *L. umbratilis*, *O. gazella*, *Phalops* sp. 1, *Onthophagus* sp. 1, *P. fossidorsis*, *O. fulgidus*, *P. femoralis*) - 1.

Scarabaeidae: Melolonthinae

LITERATURE REVIEW

Two ovaries consisting each of six ovarioles are present in *Phyllophaga anxia* (Berberet & Helms, 1972). The spermatheca is small and C-shaped and the duct is short. A rather large gland is present. The bursa copulatrix is elongated. The same structure was found by Williams (1945) who also studied species of *Phyllophaga.*

Ritcher and Baker (1974) indicated that members of Melolonthinae possess a 6-6 ovariole number. The authors dissected members of Sericini (three species), Melolonthini (10 species), Pachydemini (three species) and Macrodactylini (three species).

INTERPRETATION (FIG. 6.29; 6.30)

Number of ovarioles per side - from six to twelve. Bursa copulatrix - elongated (e.g. *Sparmannia flava* (Fig. 6.29)); varies from membranous to muscular (only in *Ptichopus angulatus*). Spermatheca and spermathecal accessory gland - elongated and membranous. Spermathecal duct - moderately long; either basally attached (two species studied, namely *Neoheteronyx cribrifrons* and in *S. flava* (Fig. 6.29)) or distally attached. Accessory glands - absent in one species, namely *P. angulatus,* but present in all other species (e.g. *Xylonichus*

eucalypti (Fig. 6.30)). Vagina varies from membranous - all studied species except *S. flava* where it is muscular.

PHYLOGENETIC INTERPRETATION

(CH9) Two ovaries per female - 0;

(CH10) six ovarioles present - 0 as well as more than six ovarioles present - 1;

(CH11) bursa copulatrix lengthened - 0;

(CH12) glandular structures absent only in *P. angulatus* - 0, but present in all other species studied - 1;

(CH13) spermathecal duct attachment varies; it is either basally attached (two species studied, namely *N. cribrifrons* and a *S. flava*) - 0 or distally attached (all other species studied) - 1.

Scarabaeidae: Rutelinae

LITERATURE REVIEW

The female genitalia of *Popillia japonica* are similar to those of the *Phyllophaga* sp. (Melolonthinae) Illustrated by Williams (1945) and. Six ovarioles are present per ovary and the bursa copulatrix is elongated. The spermathecal duct is very short, while the spermatheca and gland are comparatively shorter.

Ritcher & Baker (1974) indicated that Anomalini (five species) as well as some genera of Rutelini (10 species) possess a 6-6 ovariole number. *Cotalpa consobrina* (Rutelini) possesses 12-12 ovariole number. In the genus *Paracotalpa* two species were dissected, one species (*Paracotalpa granicollis*) possesses a 12-12 ovariole number and second species (*Paracotalpa deserta*) a 9-9 ovariole number (Ritcher & Baker, 1974).

DESCRIPTION (FIG. 6.31)

Bursa copulatrix, spermathecal accessory gland and spermatheca - elongated and membranous. Spermathecal duct - moderately long (e.g. *Anomala neoplondeus, Pelidnota notata, Lepiserica* sp. (Fig. 6.31)) to long (e.g. *Peritrichia subsquamosa*); moved distally. Accessory glands - absent in a *Lepiserica* sp. (Fig. 6.31); present in all other species - opening into bursa. Vagina - varies from membranous (e.g. *Leptohoplia testaceipennis*) to muscular (e.g. *P. subsquamosa*).

PHYLOGENETIC INTERPRETATION

(CH9) Two ovaries per female - 0;

(CH10) six ovarioles present - 0 as well as more than six ovarioles present (Ritcher & Baker, 1974) -1;

(CH11) bursa copulatrix lengthened - 0;

(CH12) glandular structures absent only in *Lepiserica* sp. - 0, but present in all other species studied - 1;

(CH13) spermathecal duct attachment is distally - 1.

Scarabaeidae: Hopliinae

LITERATURE REVIEW

Ritcher & Baker (1974) found female *Hoplia* species to possess the 6-6 ovariole number.

DESCRIPTION (FIG. 6.32; 6.33)

Six ovarioles per side - present. Bursa copulatrix, spermatheca as well as the spermathecal accessory gland - elongated and membranous (e.g. *Scelophysa militaris* (Fig.6.32) and *Pachycnema striata* (Fig. 6.33)). Spermathecal duct - moderately long and either attached basally (only *Hoplia sordita*) or distally (rest of the species studied). Accessory glands - absent (only in an *Eriesthes* sp.) and in the rest of the species opening into bursa. Vagina- always membranous.

PHYLOGENETIC INTERPRETATION

(CH9) Two ovaries per female - 0;

(CH10) six ovarioles present - 0;

(CH11) bursa copulatrix lengthened - 0;

(CH12) glandular structures absent (only in an *Eriesthes* sp.) - 0 but present in all other species studied - 1;

(CH13) spermathecal duct attachment is distally - 1.

Scarabaeidae: Dynastinae

LITERATURE REVIEW

Williams (1945) described the female genitalia of *Dynastes tityus*. Each ovary consists of six ovarioles. The bursa is an elongated structure and the entrance of the short spermathecal duct is moved distally.

The female genitalia of *Oryctes rhinoceros* were described by Mathur & Srivastava (1959). Two ovaries are present, each consisting of six ovarioles. The bursa copulatrix is thin-

walled. The spermathecal duct arises from the proximal region of the bursa. The tube is dilated in the middle, forming a chamber or spermatheca. The distal end of the tube forms the accessory gland. A genital chamber is present into which the bursa and the common oviduct opens. This chamber is just a widening of the common oviduct.

Ritcher & Baker (1974) found that females of the taxon possess a 6-6 ovariole number.

DESCRIPTION (FIG. 6.34)

Six ovarioles per side - present. Bursa copulatrix - elongated and either membranous (e.g. *Oryctes boas* (Fig. 6.34)) or muscular (e.g. *Heteronychus arator*). Spermatheca and spermathecal accessory gland - elongated and membranous. Spermathecal duct - moderately long and either attached basally (e.g. *O. boas*) or distally (e.g. *Cryptodus paradoxus*). In one species (*H. arator*) - two pairs of accessory glands are present opening into bursa. Vagina - membranous (e.g. *H. arator*) to muscular (e.g. *O. boas*).

PHYLOGENETIC INTERPRETATION

(CH9) Two ovaries per female - 0;

(CH10) six ovarioles present - 0;

(CH11) bursa copulatrix lengthened - 0;

(CH12) glandular structures are present in all species studied - 1;

(CH13) spermathecal duct attachment is either attached basally (e.g. *O. boas*) - 0 or distally (e.g. *C. paradoxus*) - 1.

Scarabaeidae: Cetoniinae

LITERATURE REVIEW

Ritcher & Baker (1974) found the females of this taxon possess ovariole numbers of 6-6 and 12-12. The 12-12 number belongs to Cetoniini, while the 6-6 number Cremastocheilini.

DESCRIPTION (FIG. 6.35)

Number of ovarioles per side - varies from six (e.g. *Plaesiorrhinella trivittata*, *Leucoscelis haemorrhoidales* and *Dischista cincta*) to nine (e.g. *Ichnestoma stobbiae*) to twelve (the rest of the species studied). Bursa copulatrix - elongated; varies from membranous (e.g. *Conastethus impressus*, *Euphoria* sp., *Dischista cincta*, *Rhabdotis semipunctata*, *Tephrala dichroa*, *Polystigma punctatum*, *Eupocila australasiae* and *Glycyphana stolata*) to muscular (e.g. *Cotinus mirabilis*, *Poecilophila hebraea* (Fig. 6.35) and *Genuchus hottentottus*). Bursa of *Lamaptera cinnamomea* - basal area muscular; distal area membranous.

Spermatheca and the spermathecal accessory gland - elongated and membranous. Spermathecal duct - moderately short and always attached distally. Accessory glands - always present; opening into bursa copulatrix. Vagina - membranous (e.g. *Oplostomus fuliginosus*) to muscular (e.g. *D. cincta*).

PHYLOGENETIC INTERPRETATION

(CH9) Two ovaries per female - 0;

(CH10) six ovarioles present - 0, more than six ovarioles present - 1;

(CH11) bursa copulatrix lengthened - 0;

(CH12) glandular structures are present in all species studied - 1;

(CH13) spermathecal duct attached distally - 1.

Scarabaeidae: Trichiinae

LITERATURE REVIEW

Ritcher & Baker (1974) found females of this taxon to possess the 6-6 (*Trichiotinis affinis*) and 12-12 (*Osmoderma eremicola*) ovariole number.

DESCRIPTION (FIG. 6.36; 6.37)

According to Ritcher & Baker (1974) the number of ovarioles per side varies from six to twelve. Bursa copulatrix - elongated; varies from membranous (e.g. *Campulipus limbatus*) to muscular (e.g. *Trigonopeltastes sallei* (Fig. 6.36)). Spermatheca and spermathecal accessory gland - both elongated and membranous. Spermathecal duct - moderately long, thick and basally attached. Accessory glands – present, opening into bursa. Vagina - varies from membranous (e.g. *C. limbatus* (Fig. 6.37)) to muscular (e.g. *T. sallei* (Fig. 6.36)).

PHYLOGENETIC INTERPRETATION

(CH9) Two ovaries per female - 0;

(CH10) six ovarioles present - 0, more than six ovarioles present -1;

(CH11) bursa copulatrix lengthened - 0;

(CH12) glandular structures are present in all species studied - 1;

(CH13) spermathecal duct attached basally - 0.

Scarabaeidae: Valginae

LITERATURE REVIEW

Ritcher & Baker (1974) found the females of one species of this taxon (*Valgus canaliculatus*) to possess a 6-6 ovariole number.

DESCRIPTION (FIG. 6.38)

Six ovarioles per side. Bursa copulatrix - elongated; muscular and sclerotised. Spermatheca and spermathecal accessory gland - elongated and membranous. Spermathecal duct - distally attached. Accessory glands - present, opening into bursa. Vagina - membranous (e.g. Valginae sp. (Fig. 6.38)).

PHYLOGENETIC INTERPRETATION

(CH9) Two ovaries per female - 0;

(CH10) six ovarioles present - 0;

(CH11) bursa copulatrix lengthened - 0;

(CH12) glandular structures are present in - 1;

(CH13) spermathecal duct attached distally - 1.

Scarabaeidae: Oncerinae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 6.39)

Number of ovarioles - unknown. Bursa copulatrix - elongated and membranous. Spermatheca and spermathecal accessory gland - elongated and membranous. Spermathecal duct - distally attached. Accessory glands - present, opening into bursa. Vagina - membranous (e.g. *Oncerus floralis* (Fig. 6.39)).

PHYLOGENETIC INTERPRETATION

(CH9) Two ovaries per female - 0;

(CH10) number of ovarioles present - 9 (missing data);

(CH11) bursa copulatrix lengthened - 0;

(CH12) glandular structures are present in - 1;

(CH13) spermathecal duct attached distally - 1.

Scarabaeidae: Chasmatopterinae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 6.40; 6.41)

Number of ovarioles per side - unknown. Bursa copulatrix, spermatheca and spermathecal accessory gland bursa (e.g. *Chnaunanthus chapini*; (Fig.6.40 and Fig. 6.41)) - elongated and membranous. Spermathecal duct - moderately long and basally attached. Accessory glands - present opening into bursa (e.g. *C. chapini* (Fig. 6.40)) . Vagina - membranous.

PHYLOGENETIC INTERPRETATION

(CH9) Two ovaries per female - 0;

(CH10) number of ovarioles present - 9 (missing data);

(CH11) bursa copulatrix lengthened - 0;

(CH12) glandular structures are present in - 1;

(CH13) spermathecal duct attached basally - 0.

Scarabaeidae: Orphninae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 6.42)

Number of ovarioles per side - unknown. Bursa copulatrix - elongated and muscular. Spermatheca and spermathecal accessory gland - elongated and membranous. Spermathecal duct - moderately long; basally attached. Accessory glands - present; opening into bursa. Vagina - muscular (e.g. *Orphnus capensis* (Fig. 6.42)).

PHYLOGENETIC INTERPRETATION

(CH9) Two ovaries per female - 0;

(CH10) number of ovarioles present - 9;

(CH11) bursa copulatrix lengthened - 0;

(CH12) glandular structures are present in - 1;

(CH13) spermathecal duct attached basally - 0.

PLATE 15

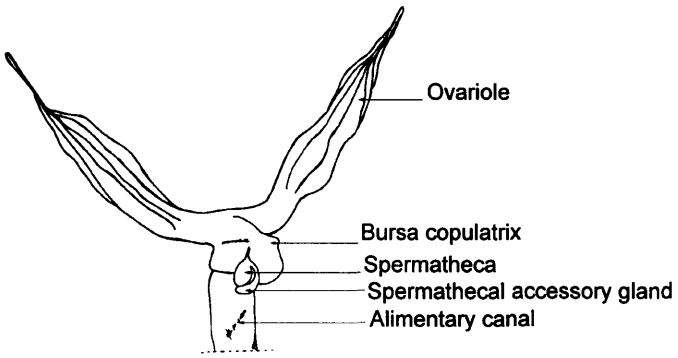


Fig. 6.1

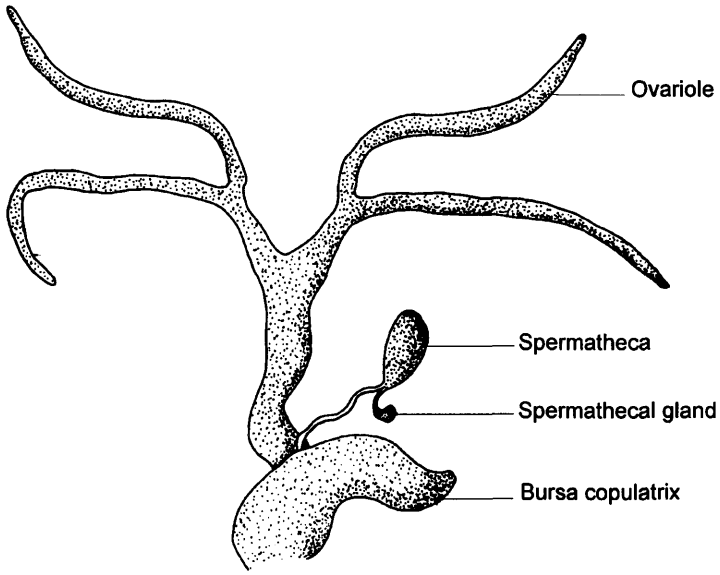


Fig. 6.2

Fig. 6.1 Internal female reproductive organs of a *Glaresis* species (Glaresidae)
Fig. 6.2 Internal female reproductive organs of *Odontotaenius disjunctus* (Passalidae)
Drawings not to scale

PLATE 16

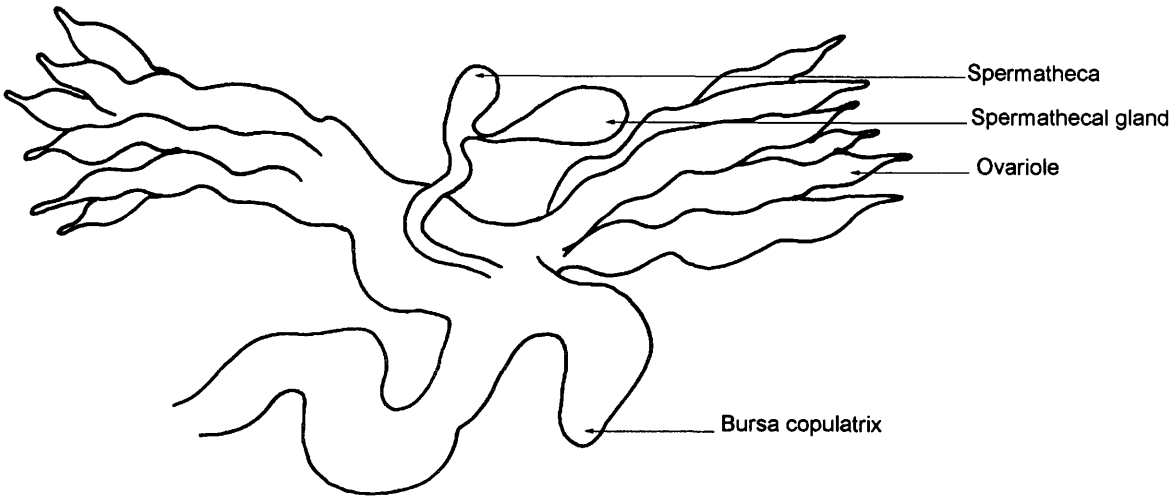


Fig. 6.3

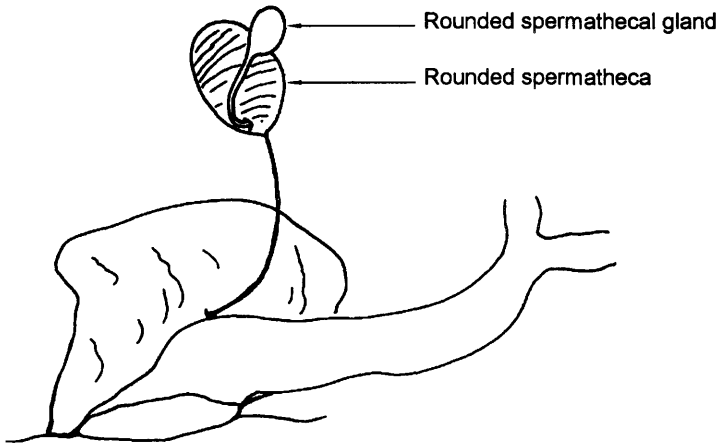


Fig. 6.4

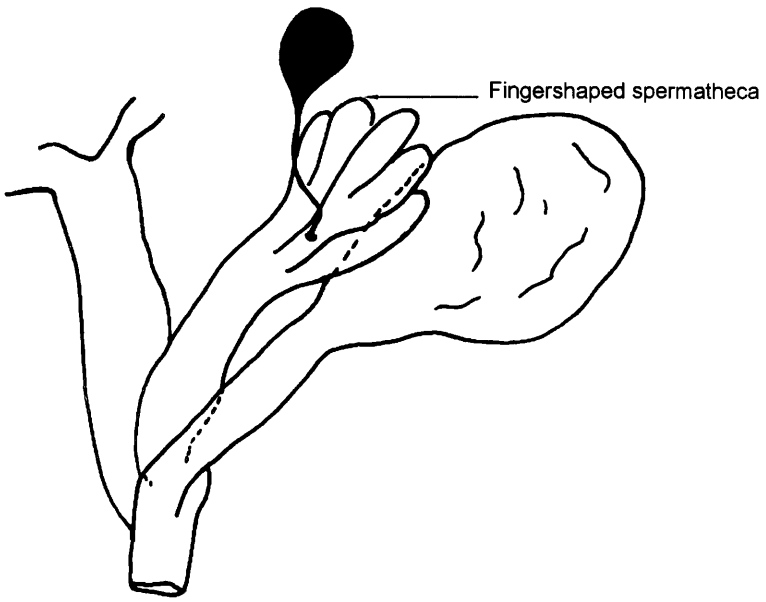


Fig. 6.5

Fig. 6.3 Internal female reproductive organs of *Syndesus cornutus* (Lucanidae)
Fig. 6.4 Bursa, spermatheca and spermathecal gland of a species of *Ceratognathus* (Lucanidae)
Fig. 6.5 Bursa, spermatheca and spermathecal gland of a species of *Rhyssonotus nebulosus* (Lucanidae)
Drawings not to scale

PLATE 17

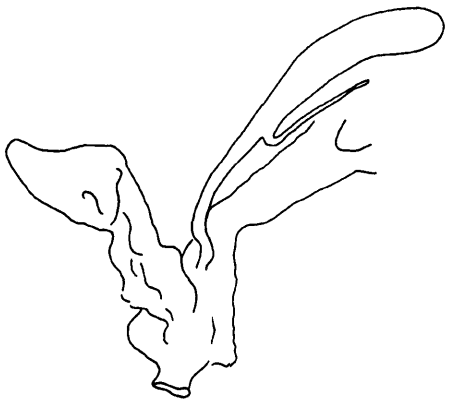


Fig. 6.6

Fig. 6.7

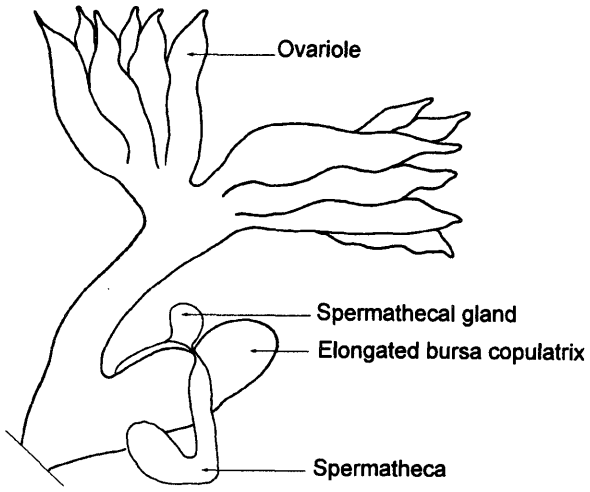


Fig. 6.8

Fig. 6.6 Bursa, spermatheca and spermathecal gland of *Sinodendron cylindricum* (Lucanidae)
Fig. 6.7 Bursa, spermatheca and spermathecal gland of *Lichnanthe apina* (Glaphyridae)
Fig. 6.8 Internal female reproductive organs of *Trox squamiger* (Trogidae)
Drawings not to scale

PLATE 18

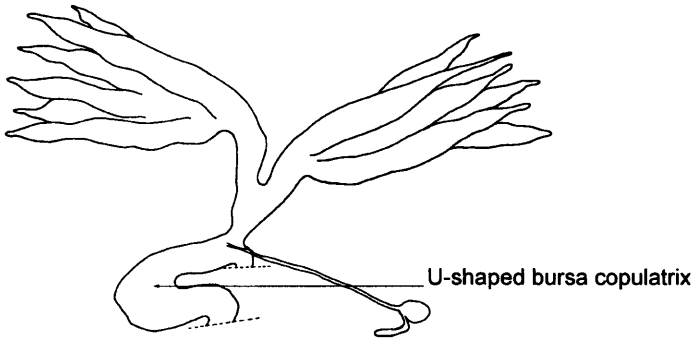
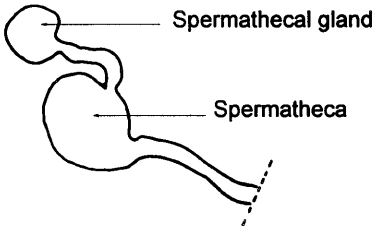


Fig. 6.9



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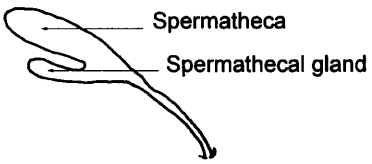


Fig. 6.11

Fig. 6.9 Internal female reproductive organs of *Omorgus asperulatus* (Trogidae)
Fig. 6.10 Spermatheca and spermathecal gland of *Omorgus suberosus* (Trogidae)
Fig. 6.11 Spermatheca and spermathecal gland of *Trox rhyparoides* (Trogidae)
Drawings not to scale

PLATE 19

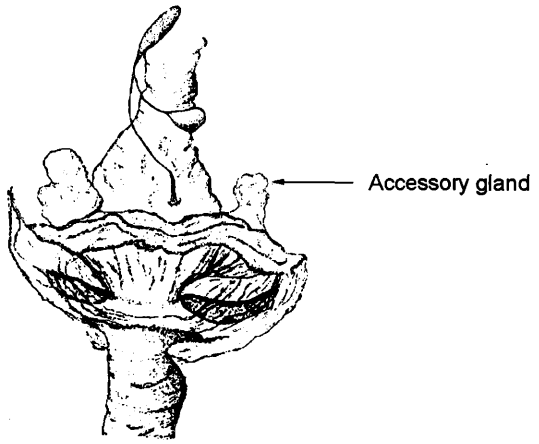


Fig. 6.12

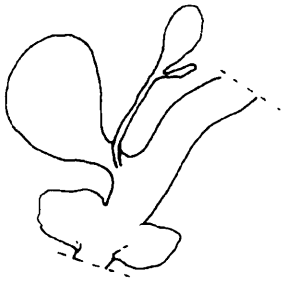


Fig. 6.13

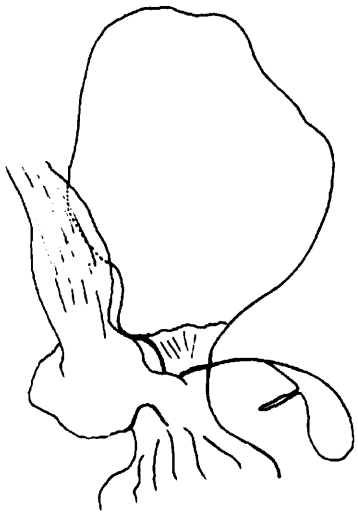
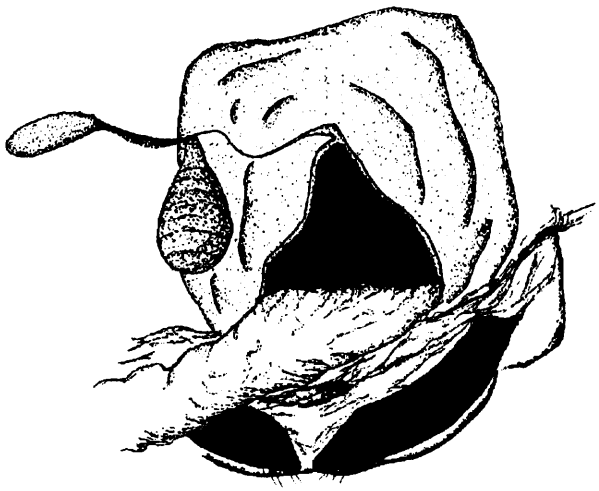


Fig. 6.14

Fig. 6.12 Bursa and ovipositor of *Bolbolaeus truncatus* (Bolboceratidae)
Fig. 6.13 Bursa, spermatheca, spermathecal gland and accessory glands of *Bolbocerus obesus* (Bolboceratidae)
Fig. 6.14 Bursa, spermatheca, spermathecal gland and accessory glands of *Pleocoma edwardsii* (Pleocomidae)
Drawings not to scale

PLATE 20



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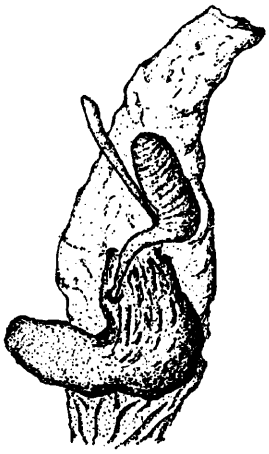

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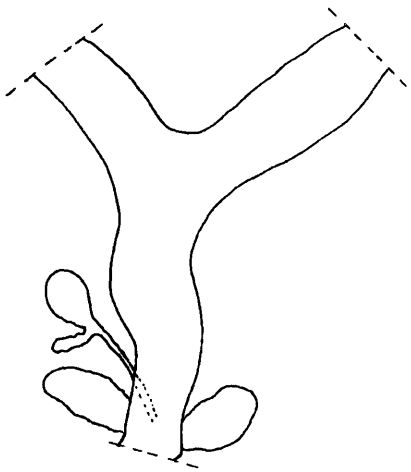


Fig. 6.17

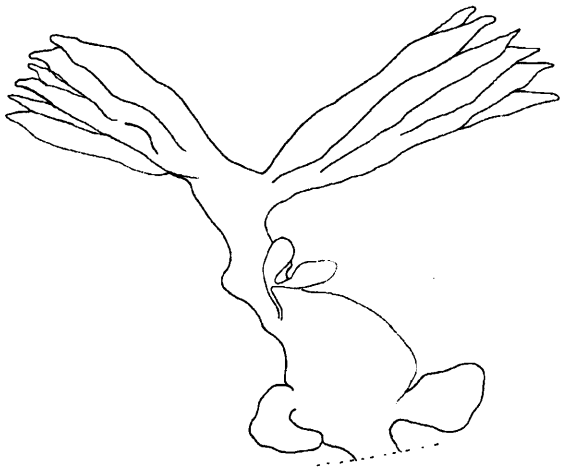


Fig. 6.18

Fig. 6.15 Bursa, spermatheca, spermathecal gland and ovipositor of *Enoplotrupes bieti* (Geotrupidae)
Fig. 6.16 Bursa, spermatheca and spermathecal gland of *Lethrus apterus* (Geotrupidae)
Fig. 6.17 Spermatheca and gland of *Mycotrupes gagei* (Geotrupidae)
Fig. 6.18 Internal female reproductive organs of *Mycotrupes gagei* (Geotrupidae)
Drawings not to scale

PLATE 21

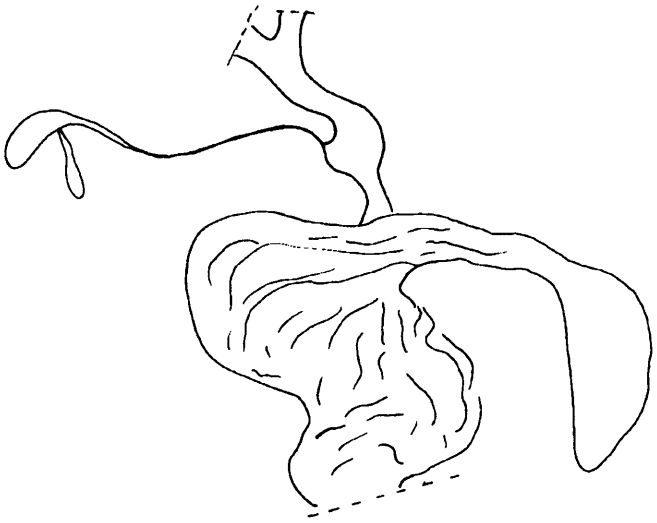


Fig. 6.19

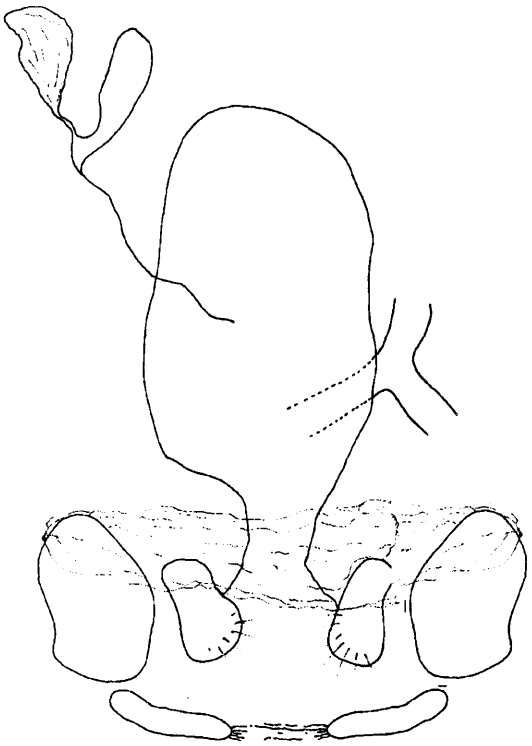
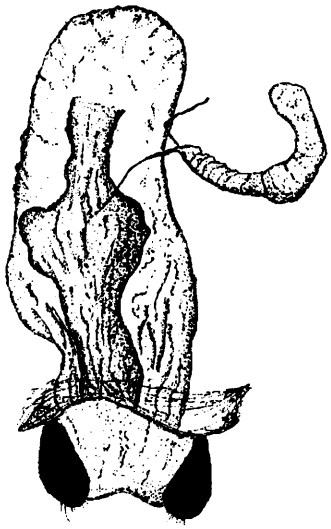


Fig. 6.20

Fig. 6.19 Bursa, spermatheca and spermathecal gland of *Ochodaeus inarmatus* (Ochodaeidae)
Fig. 6.20 Ovipositor, bursa, spermatheca and spermathecal gland of a *Cloetus* species (Ceratocanthidae)
Drawings not to scale

PLATE 22



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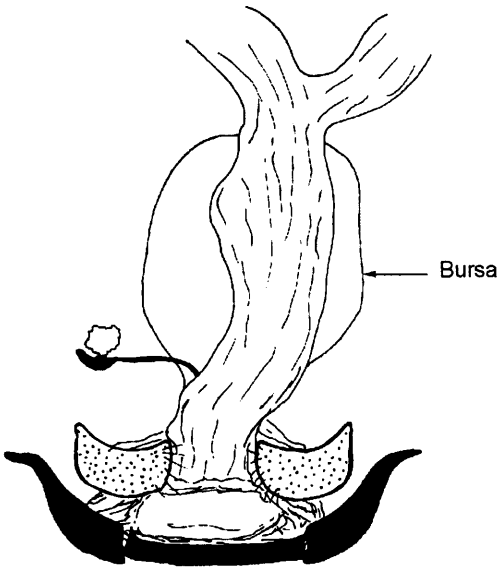

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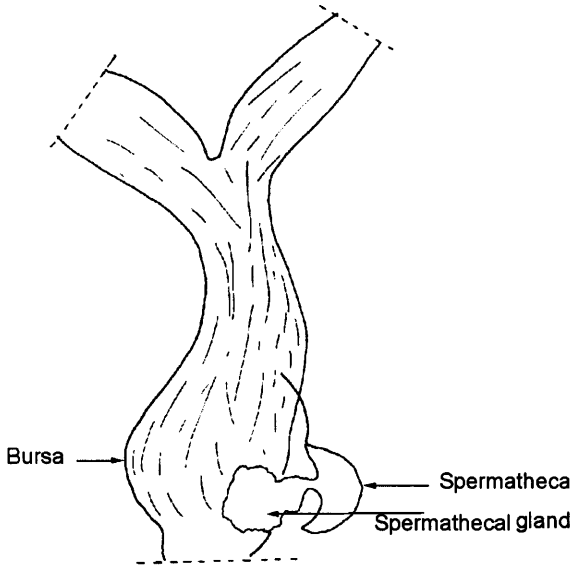
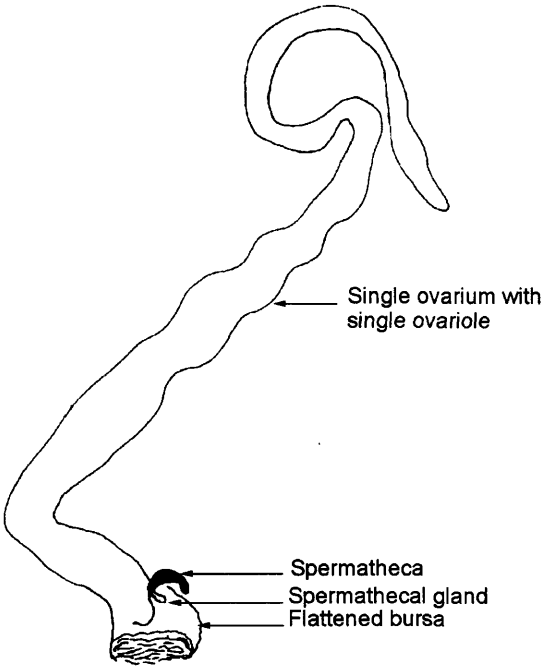


Fig. 6.23

Fig. 6.21 Bursa, spermatheca and spermathecal gland of an *Anaides* species (Hybosoridae)
Fig. 6.22 Bursa, spermatheca, spermathecal gland and ovipositor of *Aphodius tasmania* (Aphodiinae)
Fig. 6.23 Bursa, spermatheca and spermathecal gland of *Aphodius russatus* (Aphodiinae)
Drawings not to scale

PLATE 23



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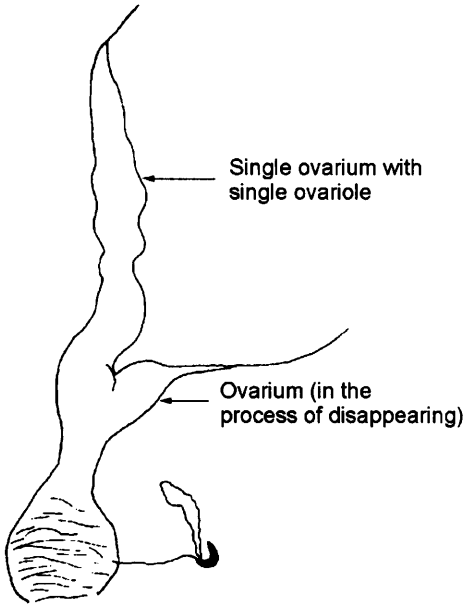

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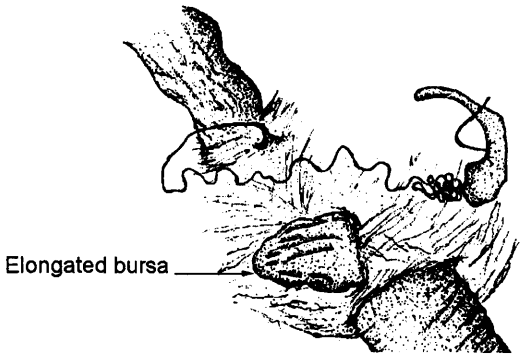


Fig. 6.26

Fig. 6.24 Single ovarium, bursa, spermatheca and spermathecal gland of *Onthophagus gazella* (Scarabaeinae)
Fig. 6.25 Internal female reproductive organs of a Pinotini species (Scarabaeinae)
Fig. 6.26 Bursa, spermatheca and spermathecal gland of *Temnoplectrum rotundum* (Scarabaeinae)
Drawings not to scale

PLATE 24

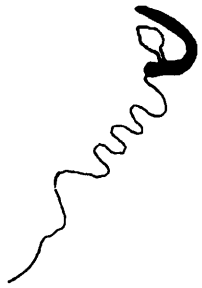
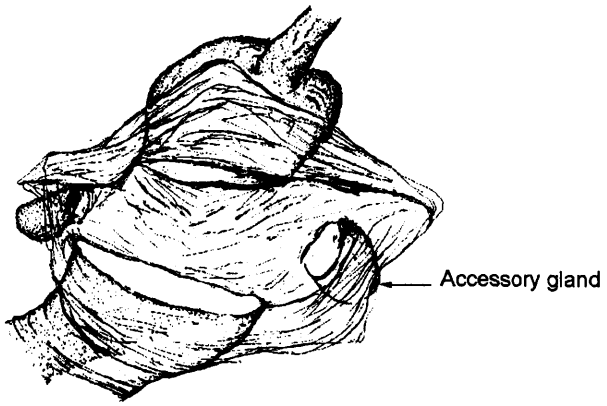


Fig. 6.27



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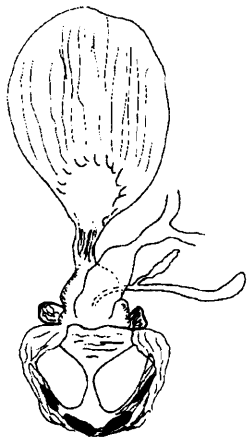


Fig. 6.29

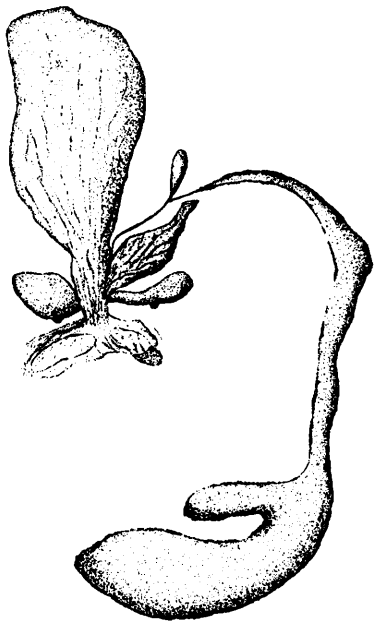


Fig. 6.30

Fig. 6.27 Spermatheca and spermathecal gland of *Labroma umbratilis* (Scarabaeinae)
Fig. 6.28 Female accessory glands of a *Copris* species (Scarabaeinae)
Fig. 6.29 Bursa, spermatheca, spermathecal gland, accessory glands and ovipositor of *Sparmania flava* (Melolonthinae)
Fig. 6.30 Bursa, spermatheca, spermathecal gland and accessory glands of *Xylonichus eucalypti* (Melolonthinae)
Drawings not to scale

PLATE 25

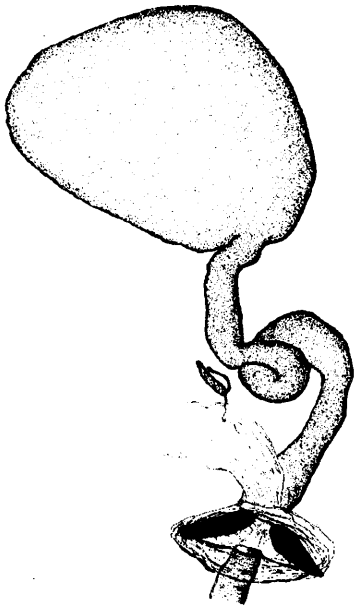


Fig. 6.31

Fig. 6.32

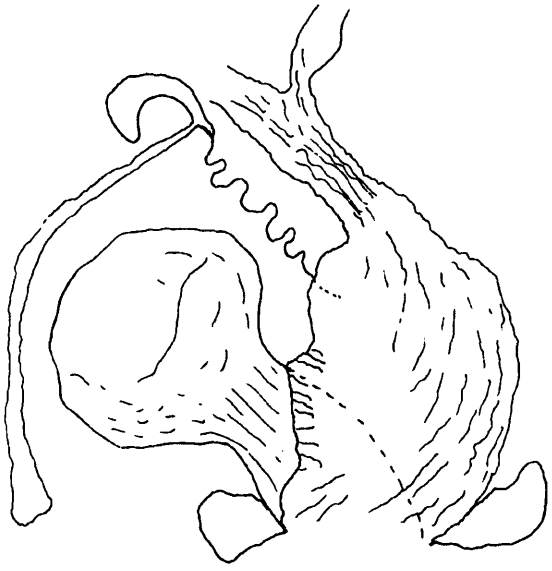


Fig. 6.33

Fig. 6.31 Bursa, spermatheca, spermathecal gland and ovipositor of a *Lepiserica* species (Rutelinae)
Fig. 6.32 Internal female reproductive organs of *Scelophysa militaris* (Hopliinae)
Fig. 6.33 Bursa, spermatheca, spermathecal gland and accessory glands of *Pachycnema striata* (Hopliinae)
Drawings not to scale

PLATE 26

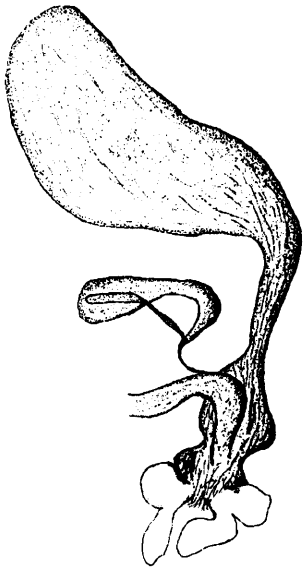


Fig. 6.34

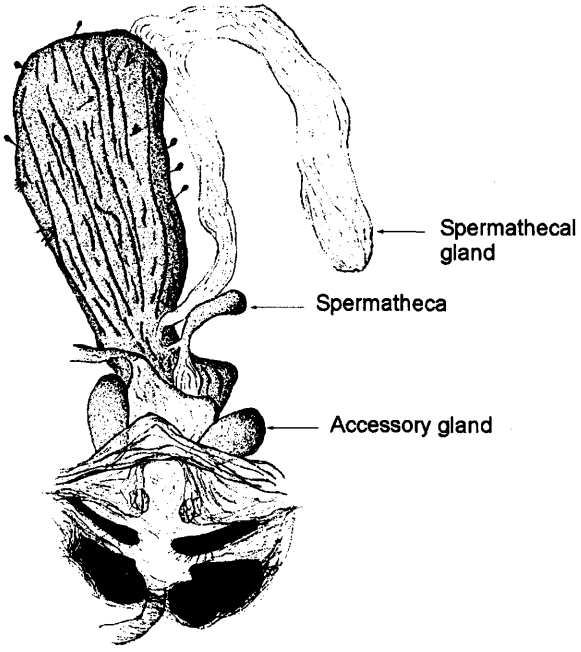
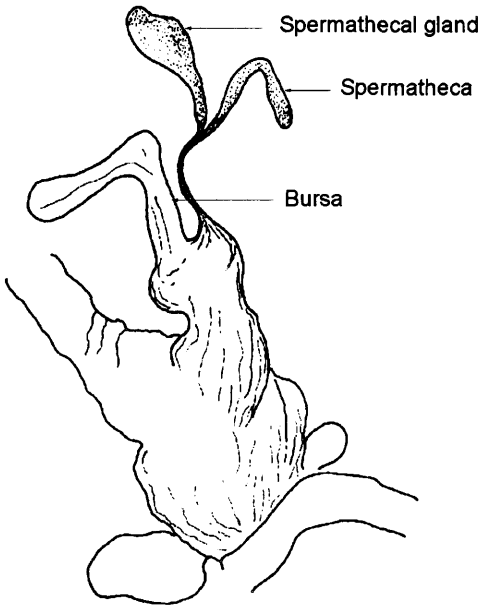


Fig. 6.35

Fig. 6.34 Bursa, spermatheca, spermathecal gland and accessory glands of *Oryctes boas* (Dynastinae)
Fig. 6.35 Bursa, spermatheca, spermathecal gland, accessory glands and ovipositor of *Poecilophila hebraea* (Cetoniinae)
Drawings not to scale

PLATE 27



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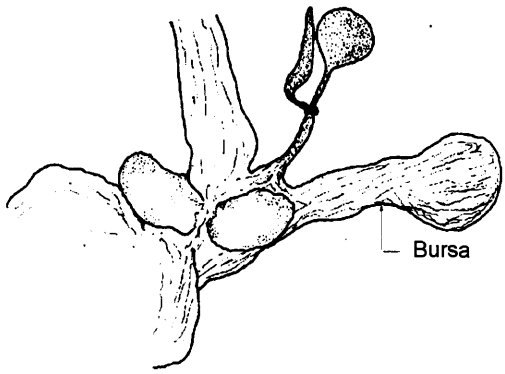

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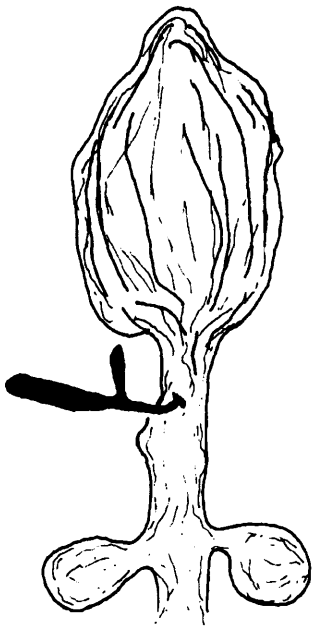


Fig. 6.38

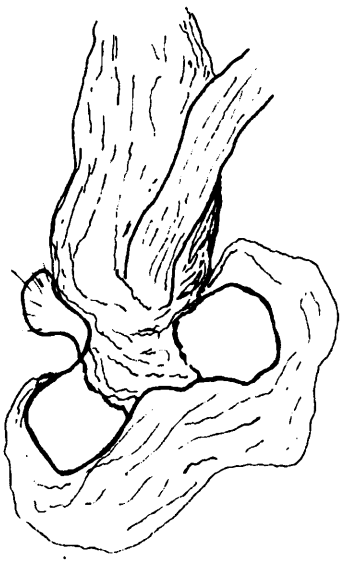


Fig. 6.39

Fig. 6.36 Bursa, spermatheca. spermathecal gland and accessory glands of *Trigonopeltastes sallei* (Trichiinae)
Fig. 6.37 Bursa, spermatheca, spermathecal gland and accessory glands of *Campulipus limbatus* (Trichiinae)
Fig. 6.38 Bursa, spermatheca, spermatheca and accessory glands of a Valginae species
Fig. 6.39 Bursa and accessory glands of *Oncerus floralis* (Oncerinae)
Drawings not to scale

PLATE 28

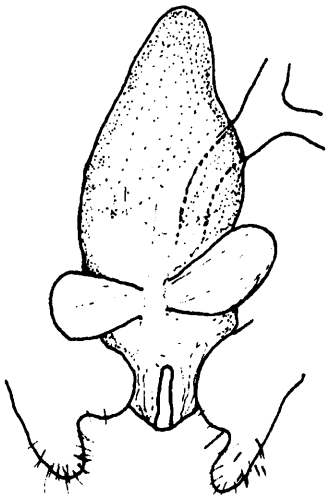


Fig. 6.40

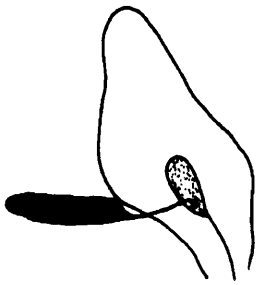


Fig. 6.41

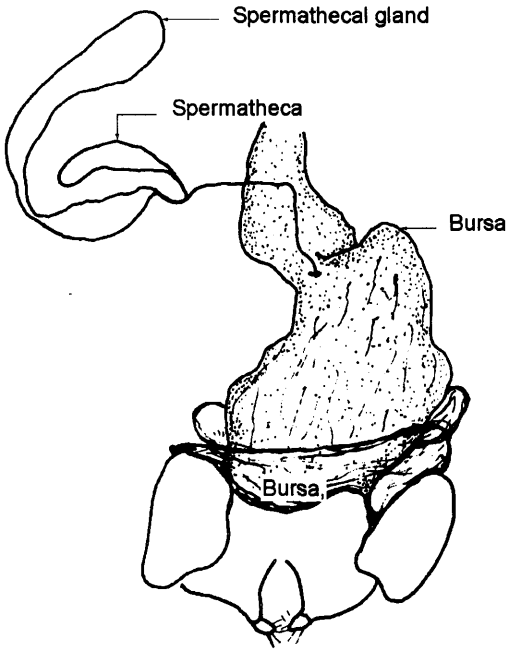


Fig. 6.42

Fig. 6.40 Bursa, accessory glands and ovipositor of *Chnaunanthus chapini* (Chasmatopterinae)
Fig. 6.41 Bursa, spermatheca and spermatheca gland of *Chnaunanthus chapini* (Chasmatopterinae)
Fig. 6.42 Bursa, spermatheca, spermatheca gland, accessory glands and ovipositor of *Orphnus capensis* (Orphninae)
Drawings not to scale

7. INTERNAL MALE REPRODUCTIVE ORGANS

Introduction

The general structure and morphology of the internal male reproductive organs were discussed in Chapter 3. Characters as well as the polarity of character states were also determined in Chapter 3. In this chapter, literature (if available) pertaining to individual families, and in the case of Scarabaeidae, subfamilies, are discussed. Morphological descriptions (of species dissected from each taxon - species dissected listed in Appendix 1.1) as well as phylogenetic interpretation of each of the identified characters, follow.

The aims of this chapter are to discuss:

- relevant literature dealing with the morphology of the internal male reproductive organs of each taxon of the Scarabaeoidea
- the morphology of the internal male reproductive organs of each taxon (results from the research done for the thesis)
- phylogenetic trends in the morphology of the internal male reproductive organs for each taxon

Glaresidae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 7.1)

Four testicular lobes per side. One pair of accessory glands - present (e.g. *Glaresis* (Fig.7.1))

PHYLOGENETIC INTERPRETATION

(CH14) less than six testicular lobes per side - 1;

(CH15) one pair of accessory glands - 0.

Passalidae

LITERATURE REVIEW

In the male genitalia of *Odontotaenius disjunctus*, both testes possess two oval bodies that

are bulbous at their distal ends (Williams, 1945). Each testicular lobe joins the vas deferens by means of vas efferens. The vasa deferentia each possess a seminal vesicle. Two pairs of accessory glands are present.

The structure of the gonads of *Passalus cornutus* was investigated by Krause (1946), and that of *Arrox agassizi* as well as *P. cornutus* by Virkki (1961). Krause concluded that the gonads of adult males consist of four testicular lobes (two per side). Each of the four lobes is a slightly elongated, cylindrical, bulb-shaped gland with a small nipple-like protuberance at the extreme distal end. The lobes are not divided into follicles. Instead, there are 20 to 30 longitudinal testicular septa extending almost the whole length of the testis from the distal to the proximal regions. A narrow duct leads from each testicular lobe to the seminal vesicle (a dilated area at the anterior end of the vas deferens). Two pairs of accessory glands are situated near the junction of the two vasa deferentia. The ejaculatory duct is long. Virkki (1961) described the same morphology for *A. agassizi*, except that he noted that no septa were present in the testes.

The testes of three species of the genus *Pentalobus* (*P. palini*, *P. barbatus* and *P. savagei*) were described by Baker (1973). Each testis is enclosed in a peritonial membrane and leading from it is a short vas deferens. Each testis consists of a single lobe. Each vas deferens is joined by two pairs of accessory glands - the posterior pair being shorter than the anterior pair and loosely coiled. The vasa deferentia and the accessory glands join at their bases and open into the rather long ejaculatory duct.

DESCRIPTION (FIG. 7.2; 7.3)

Two elongated testicular lobes per side. Vas deferens - rather short (all species); bulbous thickening in *Passalus punctiger* (Fig. 7.2) and *Odontotaenius zodiacus;* all other species studied - vas deferens of uniform thickness (e.g. *Leptaulax timorensis* (Fig. 7.3)). Two pairs of accessory glands - one shorter than the other but both without thickenings. Long, thick ductus ejaculatorius - present.

PHYLOGENETIC INTERPRETATION

(CH14) Less than six testicular lobes per side - 1;

(CH15) two pairs of accessory glands - 1.

Lucanidae

LITERATURE REVIEW

Williams (1945) found that each testis *of Pseudolucanus capreolus* to consist of twelve follicles. The vas deferens forms an epididymus below the testis, while the seminal vesicle is situated below the epididymus. Only one pair of accessory glands is present. Virkki (1961) examined the follicle structure *of Systenocerus caraboides*. The follicle is mushroom-shaped and septate. Virkki briefly mentioned that he encountered this type of follicle structure with members of *Trox*, *Onthophagus* and *Copris*. He speculated that the tendency to shorten, round out, and, finally broaden, seems to characterise the process of differentiation of the higher scarabaeoids from the primitive ones.

DESCRIPTION (FIG. 7.4)

Six testicular lobes per side - present in *Ceruchus* sp., *Nippodorcus rubrofemoratus*, *Macrodorcus rectus*, *Platyceropsis* sp. and *Syndesus cornutus* (Fig. 7.4). Twelve testicular lobes per side - present in *Prosopocoilus natalensis* and *Sinodendron rugosum*. Testicular lobes - rounded. Vas deferens - thickened and gradually becoming thinner towards the testicular lobes. One pair of accessory glands - present and of uniform thickness. Long, rather thick ductus ejaculatorius - present.

PHYLOGENETIC INTERPRETATION

(CH14) Six testicular lobes per side (e.g. *Ceruchus* sp., *N. rubrofemoratus*, *M. rectus*, *Platyceropsis* sp. and *S. cornutus*) - 0, more than six testicular lobes per side (e.g. *Prosopocoilus natalensis* and *S. rugosum*) -(unordered character state) - 1;

(CH15) one pair of accessory glands - 0.

Diphyllostomatidae

No literature available.

No males were dissected.

Glaphyridae

No literature available.

No males were dissected.

Trogidae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 7.5 – 7.7)

Six testicular lobes per side - present (e.g. *Polynoncus pedestris* (Fig.7.5)). Lobes - rounded (all *Trox* and *Polynoncus* species) (e.g. *P. pedestris* (Fig. 7.5)) or elongated - all *Omorgus* species (e.g. *Omorgus freyi* (Fig. 7.6)). One pair of accessory glands - present. Reservoir or enlarged area in the accessory gland - present. Reservoir - in the middle of the gland - all *Trox* species (e.g. *Trox squamiger* (Fig. 7.7)); at the base of the gland just before it opens into the ductus ejaculatorius in all *Polynoncus* species (e.g. *P. pedestris* (Fig. 7.5)) and slightly proximally moved from the entrance of the duct into the ductus ejaculatorius in all *Omorgus* species (e.g. *O. freyi* (Fig. 7.6)). Ductus ejaculatorius - thin and of medium length.

PHYLOGENETIC INTERPRETATION

(CH14) Six testicular lobes per side - 0;

(CH15) one pair of accessory glands - 0.

Bolboceratidae

LITERATURE REVIEW

Each testis of the male genitalia of *Bolbocerosoma farctum* possesses six oval follicles joined to the two vasa deferentia by vasa efferentia. One pair of accessory glands is present, possessing a reservoir basally (Howden & Cooper, 1977).

DESCRIPTION (FIG. 7.8; 7.9)

Six testicular lobes per side; slightly elongated (e.g. *Bolbocaffer* sp. (Fig. 7.8). Vas deferens - coiled; near entrance into the ductus ejaculatorius - widened. One pair of accessory glands; reservoir - in the middle of duct (e.g. *Bolbocaffer* sp. (Fig.7.9)). The ductus ejaculatorius is short and thick.

PHYLOGENETIC DESCRIPTION

(CH14) Six testicular lobes per side - 0;

(CH15) one pair of accessory glands - 0.

Pleocomidae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 7.10)

Eighteen round testicular lobes per side - present (e.g. *Pleocoma* sp. (Fig. 7.10)). Vas efferens, connecting each lobe to the vas deferens - long in comparison with that of the other families already mentioned. Vas deferens - long duct widening slightly near the ductus ejaculatorius. One pair of accessory glands - present. A reservoir that is wider than the rest of the duct - present just before the duct opens into the ductus ejaculatorius. Ductus ejaculatorius - thick and long.

PHYLOGENETIC INTERPRETATION

(CH14) More than six testicular lobes per side - 1;

(CH15) one pair of accessory glands - 0.

Geotrupidae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 7.11)

Six testicular lobes per side. Vas deferens - coiled. One pair of accessory glands - present (e.g. *Prototrupes copridoides* (Fig. 7.11)). Accessory glands - reservoir present - opening anterior of ductus ejaculatorius. Ductus ejaculatorius - short and thick.

PHYLOGENETIC INTERPRETATION

(CH13) Six testicular lobes per side - 0;

(CH14) one pair of accessory glands - 0.

Ochodaeidae

No literature available.

No males were dissected.

Ceratocanthidae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 7.12)

Six testicular lobes per side - present. Vas deferens - coiled. One pair of accessory glands - present. Glands - coiled; widens as it enters the ductus ejaculatorius (e.g. Ceratocanthidae sp. (Fig. 7.12)).

PHYLOGENITIC DESCRIPTION

(CH14) Six testicular lobes per side - 0;

(CH15) one pair of accessory glands - 0.

Hybosoridae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 7.13)

Six testicular lobes per side. One pair of accessory glands of uniform length - present (e.g. *Hybosorus illigeri* (Fig. 7.13)).

PHYLOGENETIC INTERPRETATION

(CH14) Six testicular lobes per side - 0;

(CH15) one pair of accessory glands - 0.

Scarabaeidae: Aphodiinae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 7.14)

Six testicular lobes per side. Vas deferens - of medium length; slightly coiled next to the testicular lobes. One pair of accessory glands - present. Accessory glands - rather long; each accessory gland widens into a reservoir just before it enters the ductus ejaculatorius. Ductus ejaculatorius - short and thick (e.g. Aphodiinae sp. (Fig. 7.14)).

PHYLOGENETIC INTERPRETATION

(CH14) Six testicular lobes per side - 0;

(CH15) one pair of accessory glands - 0.

Scarabaeidae: Scarabaeinae

LITEATURE REVIEW

Males of *Pinotus carolinus* possess two testes, each with four disc-like follicles (Williams,

1945).

DESCRIPTION (FIG. 7.15)

Six round testicular lobes per side. Vas deferens - uniform in thickness. One pair of accessory glands - present; a reservoir (or widening in the duct) - present. Ductus ejaculatorius - medium length; rather thick (e.g. *Anachalcos convexus* (Fig. 7.15)).

PHYLOGENETIC INTERPRETATION

(CH14) Six testicular lobes per side - 0;

(CH15) one pair of accessory glands - 0.

Scarabaeidae: Melolonthinae

LITERATURE REVIEW

The male genitalia of *Phyllophaga anxia* consists of two testes each consisting of six follicles, connected to the two vasa deferentia by vasa efferentia (Berberet & Helms, 1972). Paired accessory glands are present. Each vas deferens and accessory gland unite to form a single duct, united to the ductus ejaculatorius. (This was also found by Williams, 1945 for a *Phyllophaga* species.)

The male reproductive organs of *Costyletra zealandica* were described by Stringer (1990). The testis consists of six follicles each connected to the vas deferens by means of a vas efferens. A vesicula seminalis is present in each vas deferens. The paired accessory glands are long and coiled, possessing a reservoir basally.

DESCRIPTION (FIG. 7.16)

Number of testicular lobes - from six to twelve individual lobes per side. Vas deferens widens towards the ductus ejaculatorius. One pair of accessory glands - present. These glands always possess reservoirs. Ductus ejaculatorius - thick and rather short (e.g. Melolonthinae sp. (Fig. 7.16)).

PHYLOGENETIC INTERPRETATION

(CH14) Six testicular lobes per side - 0; or more than six testicular lobes per side - 1;

(CH15) one pair of accessory glands - 0.

Scarabaeidae: Rutelinae

LITERATURE REVIEW

Anderson (1950b) described the male accessory glands of *Popillia japonica*. The glands are

paired, long and coiled. The apical region tapers gradually to an expanded region at the basal portion of the gland. The expanded area continues posteriorly to where they join to receive the vasa deferentia and form the ejaculatory duct.

The male genitalia of *Popillia japonica* consist of two testes each with six oval follicles, two vasa deferentia and one pair of accessory glands, each with a reservoir basally (Williams, 1945).

DESCRIPTION (FIG. 7.17)

Six testicular lobes - present in all species studied. Each lobe - connected to each of the vas deferens by rather long vasa efferentia. Vasa deferentia - long and coiled. [It was noted (for all other species studied in this project) that in all cases where the female possesses e.g. 12 ovarioles per side, the male will possess 12 testicular lobes, it can be assumed that this would also be true for the Rutelinae (e.g. Ritcher & Baker (1974) found that *Cotalpa* (Rutelini) females possess 12-12 ovariole number and in the *Paracotalpa* one species possesses a 12-12 ovariole number and second species a 9-9 number)].

One or two pairs of very short accessory gland are present in addition to a long accessory gland of uniform thickness - found in two of the species dissected (e.g. Rutelinae sp. (Fig. 7.17)). The rest of the species studied - possess one pair of accessory glands.

PHYLOGENETIC INTERPRETATION

(CH14) Six testicular lobes per side - 0; or more than six testicular lobes per side - 1;

(CH15) one pair of accessory glands - 0; or more than one pair present (in two species studied) - 1.

Scarabaeidae: Hopliinae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 7.18)

Six testicular lobes per side - present. Vasa deferentia - long and coiled. One pair of accessory glands - present; reservoir present, close to where gland opens into the ductus ejaculatorius (e.g. *Eriesthes* sp. (Fig. 7.18)).

PHYLOGENETIC INTERPRETATION

(CH14) Six testicular lobes per side - 0;

(CH15) one pair of accessory glands - 0.

Scarabaeidae: Dynastinae

LITERATURE REVIEW

The male genitalia of *Oryctes rhinoceros* were described by Mathur & Srivastava (1959). *Oryctes rhinoceros* possesses two testes consisting of six follicles arranged in a rosette form. Due to the circular arrangement of the lobes a depression is formed in the centre of each follicle on the dorsal side. The ventral side of the testis presents a cup-shaped appearance. Each follicle is connected to the vas deferens by means of a number of fine ductiles that converge in a ventral cup-shaped area (ventral side of the testis). In the central portion of the cup-shaped area the ductiles form two thread-like ducts, the vasa efferentia. They coil around each other to form the epididymus (Snodgrass, 1935). From the epididymus two vasa deferentia from each testis arise. Each vas deferens consists of a proximal thread-like part (arising from the epididymus and gradually widens into the seminal vesicle), middle swollen part and distal narrow part. The four vasa deferentia unite and form a common duct, the ejaculatory duct.

DESCRIPTION (FIG. 7.19)

Twelve testicular lobes per side - present. Vas deferens - coiled and long. One pair of accessory glands - present; forming a reservoir or enlarged area just before entering the ductus ejaculatorius (e.g. Dynastinae sp. (Fig. 7.19)).

PHYLOGENETIC INTERPRETATION

(CH14) More than six testicular lobes per side - 1;

(CH15) one pair of accessory glands - 0.

Scarabaeidae: Cetoniinae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 7.20; 7.21)

Where the females of the species possess six ovarioles per side, (e.g. *Leucoscelis haemorrhoidales*, *Dischista cincta* and *Plaesiorrhinella trivittata*) the males also possess six testicular lobes per side. The males of *Ichnestoma stobbiae,* however, possess twelve testicular lobes per sided (females possess 9 ovarioles per side). All other male specimens studied - twelve testicular lobes per side (e.g. *Diplognatha silicea* (Fig. 7.20)). Number of

accessory glands - varies from one pair (e.g. *Raceloma jansoni* (Fig. 7.21)) two (e.g. *Ichnestoma stobbiae)* to three pairs (e.g. *Hypselogenia geotrupina*, *Eudicella smithii*, *Anisorrhina flavomaculata*, *P. trivittata* and *D. silicea* (Fig. 7.20)).

PHYLOGENETIC INTERPRETATION

(CH14) Six testicular lobes per side - 0 more than six testicular lobes per side - 1;

(CH15) one pair of accessory glands - 0, also more than one pair present - 1.

Scarabaeidae: Trichiinae, Valginae, Oncerinae, Chasmatopterinae and Orphninae

No literature available.

No fresh male specimens were dissected.

PLATE 29

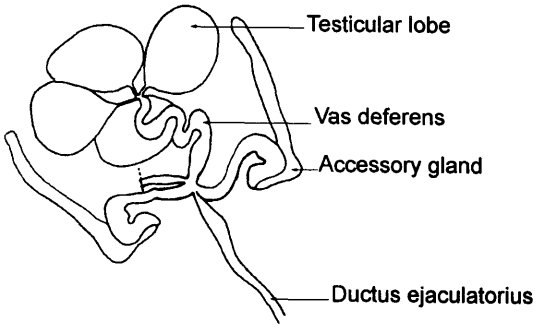


Fig. 7.1

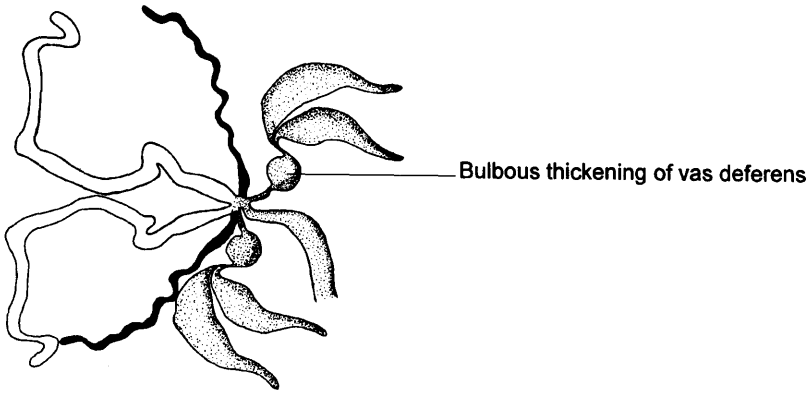


Fig. 7.2

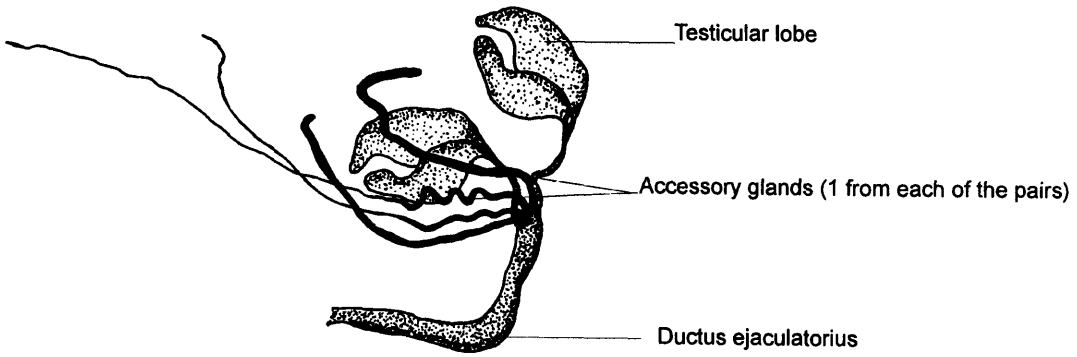


Fig. 7.3

Fig. 7.1 Internal male reproductive organs of a *Glaresis* species (Glaresidae)
Fig. 7.2 Internal male reproductive organs of *Passalus punctiger* (Passalidae)
Fig. 7.3 Internal male reproductive organs of *Leptaulax timorensis* (Lucanidae)
Drawings not to scale

PLATE 30

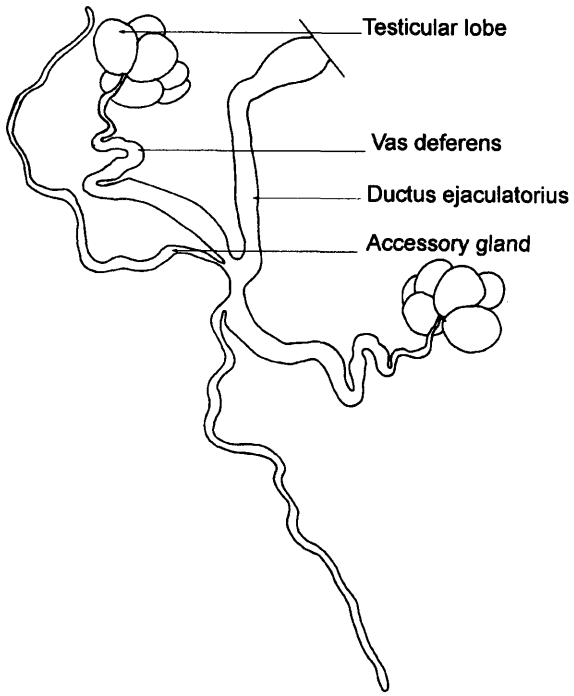


Fig. 7.4

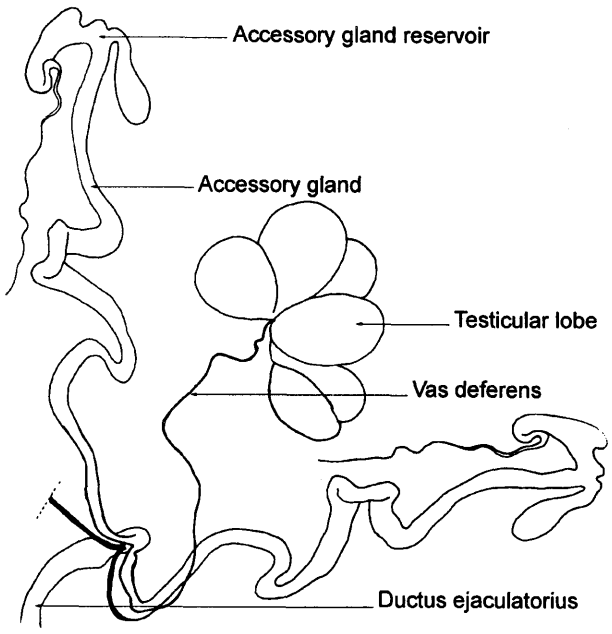


Fig. 7.5

Fig. 7.4 Internal male reproductive organs of *Syndesus comutus* (Lucanidae)
Fig. 7.5 Internal male reproductive organs of *Polynoncus pedestris* (Trogidae)
Drawings not to scale

PLATE 31

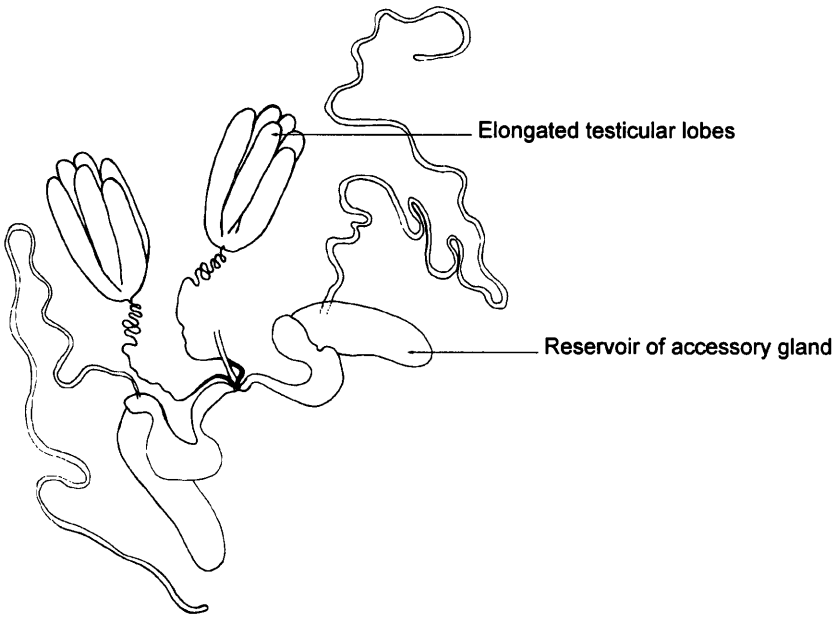


Fig. 7.6

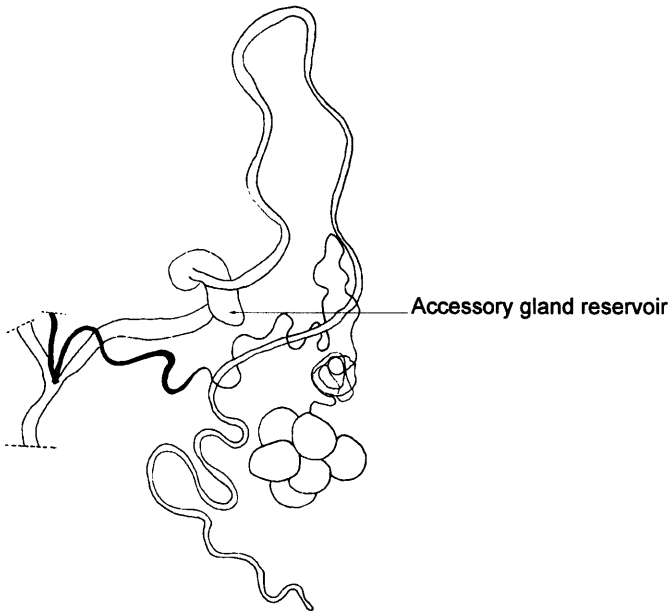


Fig. 7.7

Fig. 7.6 Internal male reproductive organs of *Omorgus freyi* (Trogidae)
Fig. 7.7 Internal male reproductive organs of *Trox squamiger* (Trogidae)
Drawings not to scale

PLATE 32

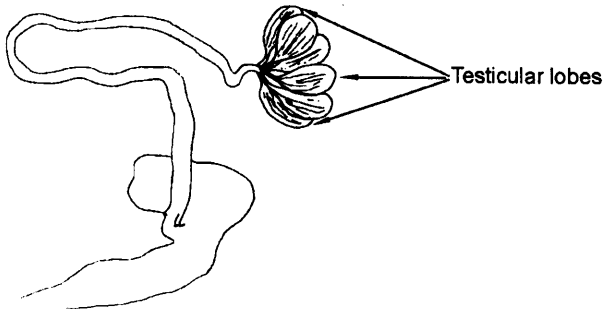


Fig. 7.8

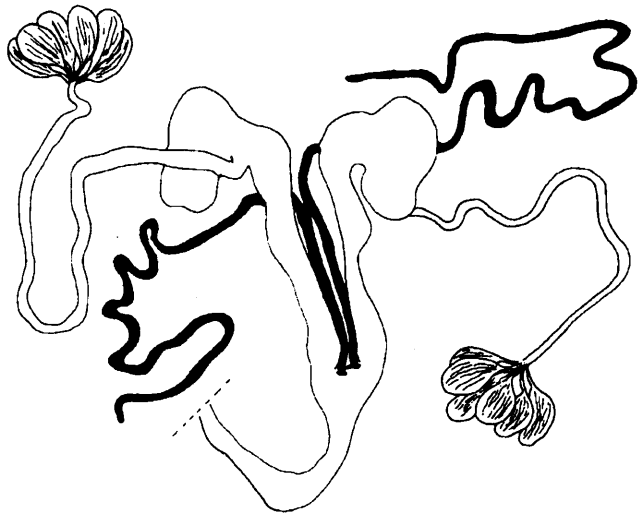


Fig. 7.9

Fig. 7.8 Six testicular lobes of a *Bolbocaffer* species (Bolboceratidae)
Fig. 7.9 Male internal reproductive organs of a *Bolbocaffer* species (Bolboceratidae)
Drawings not to scale

PLATE 33

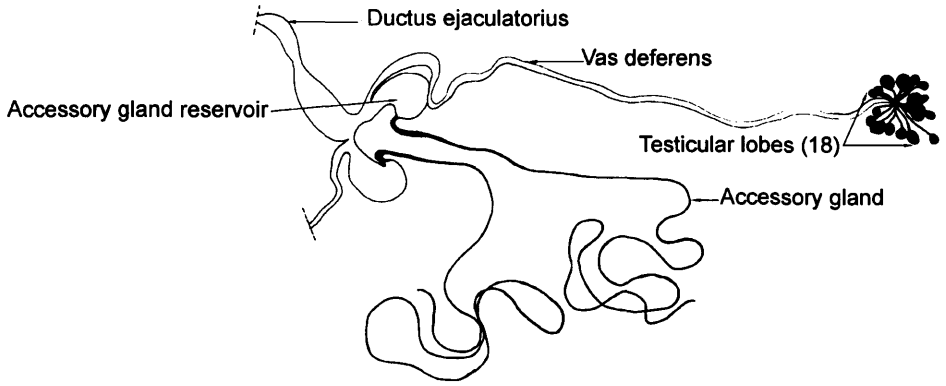


Fig. 7.10

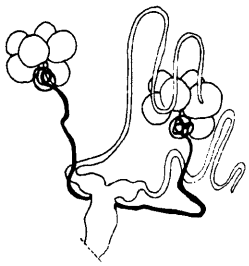


Fig. 7.11

Fig. 7.12

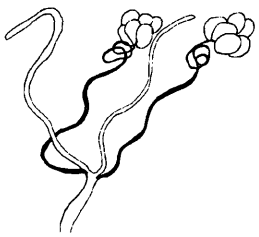


Fig. 7.13

Fig. 7.10 Internal male reproductive organs of a *Pleocoma* species (Pleocomidae)
Fig. 7.11 Internal male reproductive organs of *Prototrupes capridoides* (Geotrupidae)
Fig. 7.12 Internal male reproductive organs of an unidentified Ceratocanthidae species
Fig. 7.13 Internal male reproductive organs of *Hybosorus illigeri* (Hybosoridae)
Drawings not to scale

PLATE 34

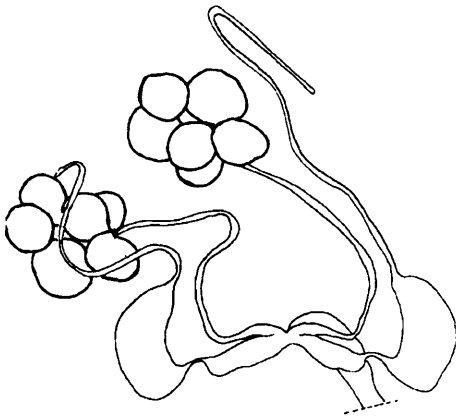


Fig. 7.14

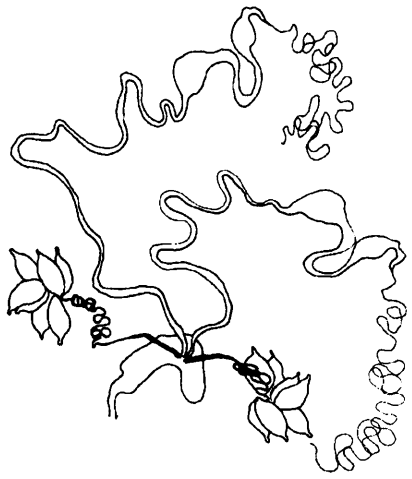


Fig. 7.15

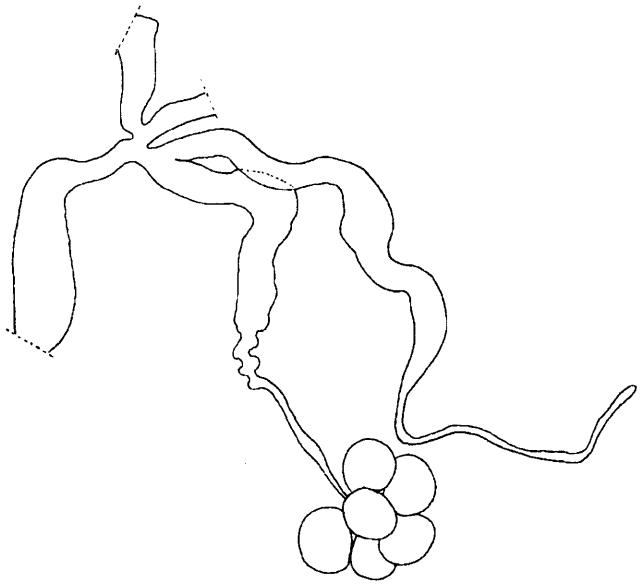


Fig. 7.16

Fig. 7.14 Internal male reproductive organs of an *Aphodius* species (Aphodiinae)
Fig. 7.15 Internal male reproductive organs of *Anachalcos convexus* (Scarabaeinae)
Fig. 7.16 Internal male reproductive organs of an unidentified Melolonthinae species
Drawings not to scale

PLATE 35

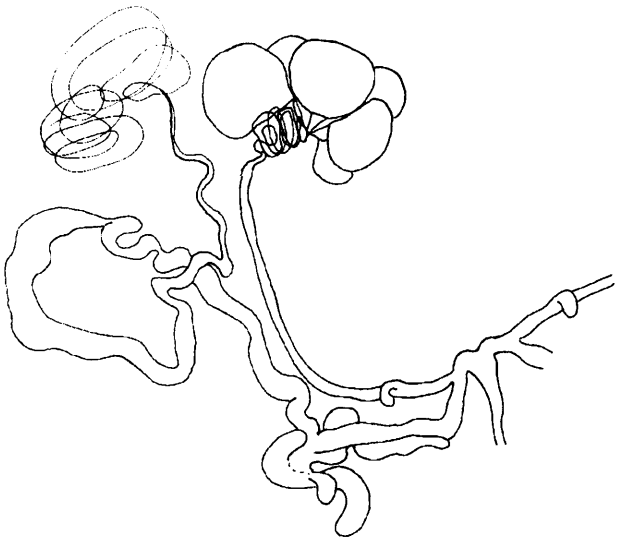


Fig. 7.17

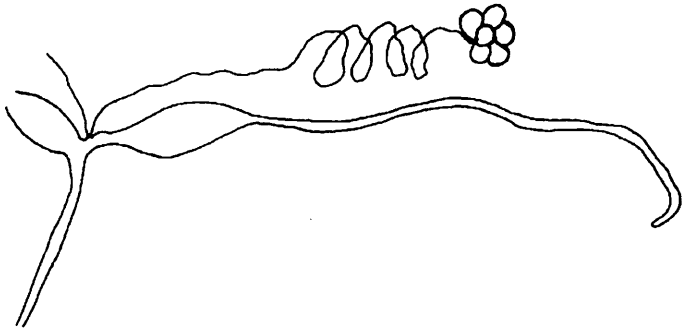


Fig. 7.18

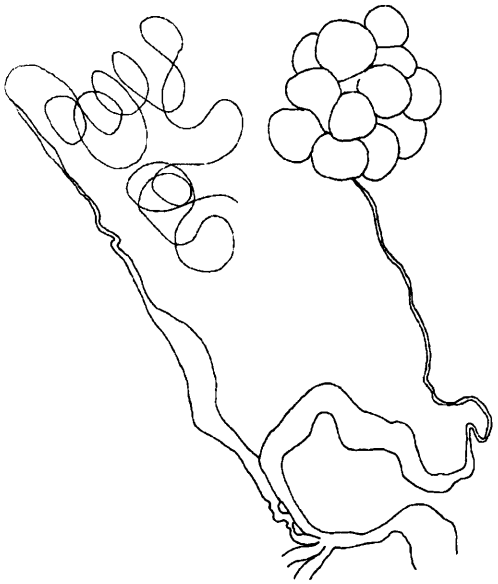


Fig. 7.19

Fig. 7.17 Internal male reproductive organs of an unidentified Rutelinae species
Fig. 7.18 Internal male reproductive organs of an unidentified Hopliinae species
Fig. 7.19 Internal male reproductive organs of *Oryctes boas* (Dynastinae)
Drawings not to scale

PLATE 36

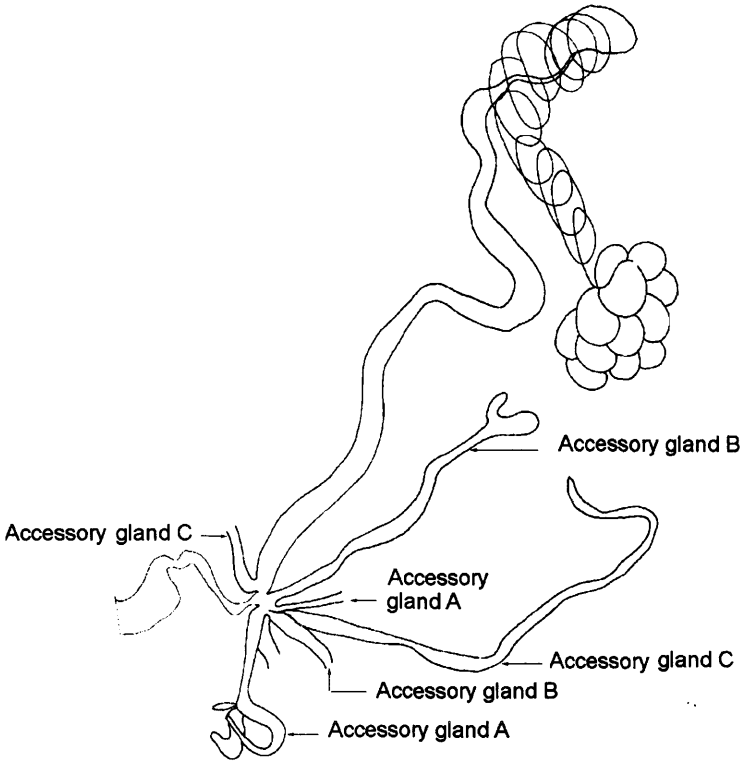


Fig. 7.20

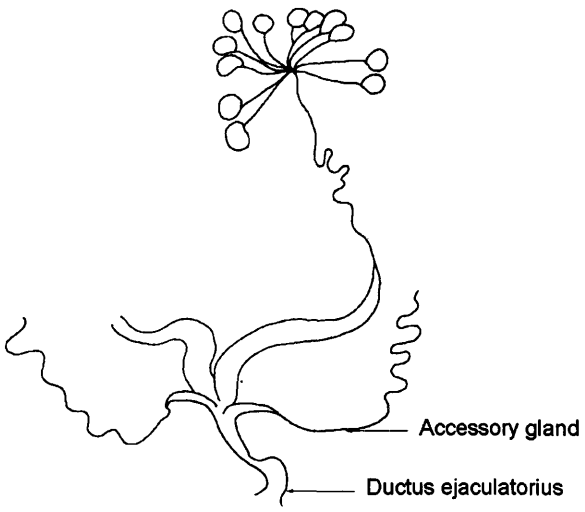


Fig. 7.21

Fig. 7.20 Internal male reproductive organs of *Diplognatha silicea* (Cetoniinae)
Fig. 7.21 Internal male reproductive organs of *Raceloma jansoni* (Cetoniinae)
Drawings not to scale

8. OVIPOSITOR

Introduction

The general structure and morphology of the ovipositor were discussed in Chapter 3. Characters as well as the polarity of character states were also determined in Chapter 3. In this chapter, literature (if available) pertaining to individual families, and in the case of Scarabaeidae, subfamilies, are discussed. Morphological descriptions (of species dissected from each taxon - species dissected listed in Appendix 1.1) as well as phylogenetic interpretation of each of the identified characters, follow.

The aims of this chapter are to discuss:

- relevant literature dealing with the morphology of the ovipositor of each taxon of the Scarabaeoidea
- the morphology of the ovipositor of each taxon (results from the research done for the thesis)
- phylogenetic trends in the morphology of the ovipositor for each taxon.

Glaresidae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 8.1)

Ovipositor present. Paired hemisternites and paired sternites – present but separate. Tergite - undivided (e.g. *Glaresis* sp. (Fig. 8.1)).

PHYLOGENETIC INTERPRETATION

(CH16) Ovipositor present - 0;

(CH17) paired hemisternites and paired sternites separate - 0;

(CH18) tergite undivided - 0.

Passalidae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 8.2)

Ovipositor - present. Paired hemisternites and sternites - united and undivided. Styli - not present. Tergite - undivided (e.g. *Odontotaenius disjunctus* (Fig. 8.2)).

PHYLOGENETIC INTERPRETATION

(CH16) Ovipositor present - 0;

(CH17) hemisternites and sternites united and undivided - 1;

(CH18) tergite undivided - 0.

Lucanidae

LITERATURE REVIEW

Holloway (1961) investigated the taxonomy of the four genera of Lucanidae and studied, amongst other characters, the female ovipositor. She examined species belonging to: *Dendroblax* (1 species), *Dorcus* (6 species), *Ceratognathus* (10 species) and *Lissotes* (6 species). Paired hemisternites with styli were present in all the taxa studied. According to Holloway, the styli and hemisternites exhibit a considerable amount of intraspecific variation in shape and therefore have limited taxonomic value.

Throughout Lucanidae tergite 9, pleurite 9, and sternite 9 are represented by sclerotised areas, and hemisternites, usually with well-developed styli (Holloway, 1972).

DESCRIPTION (FIG. 8.3)

Ovipositor - always present. Paired hemisternites with styli - present. Paired sternites - present. Tergite - undivided (e.g. Lucanidae sp. 1 (Fig. 8.3)).

PHYLOGENETIC INTERPRETATION

(CH16) ovipositor present - 0;

(CH17) hemisternites and sternites separate - 0;

(CH18) tergite undivided - 0.

Diphyllostomatidae

LITERATURE REVIEW

There is a progressive loss in sclerotised areas of the ovipositor. The hemisternites are fused to the sternites that are divided; no styli are present. The tergite is undivided (Holloway, 1972).

DESCRIPTION

No females dissected.

PHYLOGENETIC INTERPRETATION (ACCORDING TO HOLLOWAY, 1972)

(CH16) Ovipositor present - 0;

(CH17) sternites and hemisternites united and combined structure divided - 2;

(CH18) tergite undivided - 0.

Glaphyridae

LITERATURE REVIEW

Holloway (1972) briefly discussed the ovipositor of the Glaphyridae. According to her, the ovipositor of this taxon resembles that of the Lucanidae. Tergite 9, pleurite 9, and sternite 9 are represented by sclerotised areas, and the hemisternites usually possess well-developed styli.

DESCRIPTION (FIG. 8.4)

Ovipositor - present. Hemisternites and sternites - united forming one structure. Tergite - divided by a membranous area in the middle (e.g. *Lichnanthe rathvoni* (Fig. 8.4)).

PHYLOGENETIC INTERPRETATION

(CH16) Ovipositor present - 0;

(CH17) hemisternites and sternites not divided - 1;

(CH18) tergite divided - 1

Trogidae

LITERATURE REVIEW

Holloway (1972) briefly discussed the ovipositor of Trogidae. According to her, the ovipositor of this taxon also resembles that of the Lucanidae. Tergite 9, pleurite 9, and sternite 9 are represented by sclerotised areas, and the hemisternites usually possess well-developed styli.

DESCRIPTION (FIG. 8.5)

Ovipositor - present. Hemisternites and sternites - united. Tergite - divided by a membranous area (e.g. *Omorgus asperulatus* (Fig. 8.5)).

PHYLOGENETIC INTERPRETATION

(CH16) Ovipositor present - 0;

(CH17) hemisternites and sternites united - 1;

(CH18) tergite is divided - 1.

Bolboceratidae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 8.6)

Ovipositor - present. Sternites - united to the hemisternites. Tergite - undivided (e.g. *Elephastomus meraldus* (Fig.8.6)).

PHYLOGENETIC INTERPRETATION

(CH16) Ovipositor present - 0;

(CH17) hemisternites and sternites united - 1;

(CH18) tergite undivided - 0.

Pleocomidae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 8.7; 8.8)

Ovipositor - present. Hemisternites - present. Styli - present in *Pleocoma edwardsii* (Fig. 8.7) but absent in *Pleocoma dubitabilis* (Fig. 8.8). Sternites - small. Tergite - undivided (lightly sclerotised in *P. dubitabilis* and not sclerotised in *P. edwardsii*).

PHYLOGENETIC INTERPRERETATION

(CH16) Ovipositor present - 0;

(CH17) hemisternites and sternites present - 0;

(CH18) tergite undivided - 0.

Geotrupidae

LITERATURE REVIEW

Holloway (1972) briefly discussed the ovipositor of Geotrupidae (*Elephastomus proboscideas* and a *Geotrupes* species). She mentioned that more specialised Scarabaeoidea show a progressive reduction of the sclerotised areas. The Geotrupidae do not possess hemisternites, their function being taken over by the modified sternite of segment 9.

Bovo & Zunino (1993) described the ovipositor of four species of Geotrupidae, and

mentioned specifically the structure and form of the pleurite and tergite to compare the species. Zunino (1984) examined 23 genera belonging to Geotrupidae and also mentioned the structure and form of the pleurite and tergite to help with the systematic analysis of the studied group. The ovipositor of the group basically consists of a sclerotised tergite, not divided by a membranous area with the two pleurites situated next to the tergite (one on each side).

DESCRIPTION (FIG. 6.15; 8.9; 8.10)

Ovipositor - present. Sternites and hemisternites - present (e.g. *Lethrus apterus* (Fig. 8.9) and *Enoplutrupes bieti* (Fig, 6.19)). Tergite - divided (only in *Frickius variolosus (*Fig. 8.10)*;* tergite - divided by membranous middle part) to undivided (all other species studied).

PHYLOGENETIC INTERPRETATION

(CH16) Ovipositor present - 0;

(CH17) hemisternites and sternites united but not divided - 1;

(CH18) tergite undivided - 0 to divided - 1.

Ochodaeidae

LITERATURE REVIEW

Holloway (1972) briefly discussed the ovipositor of Ochodaeinae as a subfamily of Hybosoridae. According to her, the ovipositor of this taxon also resembles that of the Lucanidae and Trogidae. Tergite 9, pleurite 9, and sternite 9 are represented by sclerotised areas, and the hemisternites usually possess well-developed styli.

DESCRIPTION (FIG. 8.11)

Ovipositor - present. Hemisternites and sternites - present; not divided. The tergite - undivided membranous (e.g. *Ochodaeus inarmatus* (Fig. 8.11)).

PHYLOGENETIC INTERPRETATION

(CH16) Ovipositor present - 0;

(CH17) hemisternites and sternites separate - 0;

(CH18) tergite not divided - 0.

Ceratocanthidae

LITERATURE REVIEW

Holloway (1972) briefly discussed the ovipositor of Ceratocanthidae. According to her, the ninth tergite has become completely membranous along the midline (e.g. *Cloeotus* sp.).

DESCRIPTION (FIG. 6.20)

Ovipositor - present. Hemisternites and sternites - united and undivided. Tergite - divided by a membranous area (e.g. *Cloetus* sp. (Fig. 6.20)).

PHYLOGENETIC INTERPRETATION

(CH16) Ovipositor present - 0;

(CH17) hemisternites and sternites united but not divided - 1;

(CH18) tergite divided - 1.

Hybosoridae

LITERATURE REVIEW

Holloway (1972) briefly discussed the ovipositor of Hybosoridae. According to her, the ninth tergite has become completely membranous along the midline (e.g. *Phaeochrous* sp.).

DESCRIPTION (FIG. 6.21; 8.12)

Ovipositor - present. Hemisternites and sternites - united and undivided (e.g. *Anaides* sp. (Fig. 6.21)). *Liparochrus hackeri* (Fig. 8.12) - possesses hemisternites with styli, (but it seems as if they are united to the sternites, as long, thin cuticular "strips" leaving the hemisternites anteriorly). Tergite - divided.

PHYLOGENETIC INTERPRETATION

(CH16) Ovipositor present - 0;

(CH17) hemisternites and sternites are united but not divided - 1;

(CH18) tergite divided - 1.

Scarabaeidae: Aphodiinae

LITERATURE REVIEW

Holloway (1972) briefly discussed the ovipositor of the Aphodiinae. According to her, the tergite is weakly sclerotised in the vacinity of the midline.

DESCRIPTION (FIG. 8.13)

Ovipositor - present. Hemisternites and sternites - united and undivided. Tergite - divided (e.g. *Ataenius* sp. (Fig. 8.13)).

PHYLOGENETIC INTERPRETATION

(CH16) Ovipositor present - 0;

(CH17) hemisternites and sternites united but not divided - 1;

(CH18) tergite divided - 1.

Scarabaeidae: Scarabaeinae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 8.14; 8.15)

The Scarabaeinae is the only group with some members not having sclerotised parts (sternites, pleurites and tergites) forming an ovipositor (e.g. *Diatellopalpus thomsoni* (Fig. 8.14)). Five species belonging to Onthophagini were studied - in four of the species the ovipositor sclerites - absent (present only in *Onthophagus gazella*). Ovipositor sclerites present - (e.g. *Proagoderus fossidorsis* (Fig. 8.15)) One species belonging to Scarabaeini, (*Labroma umbratilis)* - no ovipositor sclerites present.

When present - ovipositor consists of hemisternites and sternites (united but undivided). Tergite - divided (Fig. 8.17).

PHYLOGENETIC INTERPRETATION

(CH16) Ovipositor present - 0; absent (only in *L. umbratilis*, *D. thomsoni*, *O. gazella*, *Phalops* sp. 1, *Onthophagus* sp.) - 1;

(CH17) hemisternites and sternites fused - 1;

(CH18) tergite divided by membranous area - 1.

Scarabaeidae: Melolonthinae

LITERATURE REVIEW

Holloway (1972) briefly discussed the ovipositor of Melolonthinae. According to her, the ninth tergite has become completely membranous.

DESCRIPTION (FIG. 6.29; 8.16)

Ovipositor - always present (e.g. *Sparmannia flava* (Fig. 6.29)). Hemisternites and sternites - united and undivided but in one species, *Schizonycha puncticollis* (Fig. 8.16) the united structure - again divided. Tergite - divided by a membranous area.

PHYLOGENETIC INTERPRETATION

(CH16) Ovipositor present - 0;

(CH17) hemisternites and sternites fused and undivided - 1 but in *Schizonycha puncticollis* the united structure is again divided - 2;

(CH18) tergite divided by membranous area - 1.

Scarabaeidae: Rutelinae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 8.17)

Ovipositor - present. Hemisternites and sternites - united and undivided (e.g. *Adoretus variegatus*) or divided (e.g. *Peritrichia subsquamosa* (Fig. 8.17)). Tergite - divided by a membranous area.

PHYLOGENETIC INTERPRETATION

(CH16) Ovipositor present - 0;

(CH17) hemisternites and sternites are united and undivided (e.g. *A. variegatus*) - 1 or divided (e.g. *P. subsquamosa, Amocrates* sp.) - 2;

(CH18) tergite divided by membranous area - 1.

Scarabaeidae: Hopliinae

DESCRIPTION (FIG. 8.18)

Ovipositor - present. Hemisternites and sternites - united and divided. Tergite - divided (e.g. *Eriesthes* sp. (Fig. 8.18)).

PHYLOGENETIC INTERPRETATION

(CH16) Ovipositor present - 0;

(CH17) hemisternites and sternites are united and divided - 2;

(CH118) tergite divided by membranous area - 1.

Scarabaeidae: Dynastinae

LITERATURE REVIEW

Holloway (1972) briefly discussed the ovipositor of Dynastinae. According to her, the ninth tergite has become completely membranous.

DESCRIPTION (FIG. 8.19)

Ovipositor - present. Hemisternites and sternites - united and divided. Tergite - divided by a membranous area (e.g. *Heteronychus arator* (Fig. 8.19)).

PHYLOGENETIC INTERPRETATION

(CH16) Ovipositor present - 0;

(CH17) hemisternites and sternites are united and divided - 2;

(CH18) tergite divided by membranous area - 1.

Scarabaeidae: Cetoniinae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 8.20)

Ovipositor - always present. Hemisternites and sternites - united and undivided; or divided (only *Lamaptera cinnamomea (*Fig. 8.20)). Tergite - divided by a membranous area.

PHYLOGENETIC INTERPRETATION

(CH16) Ovipositor present - 0;

(CH17) hemisternites and sternites are united undivided - 1 or united and divided - 2;

(CH18) tergite divided by membranous area - 1.

Scarabaeidae: Trichiinae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 8.21)

Ovipositor - present. Hemisternites and sternites - united and divided. Tergite - divided (e.g. *Campulipus limbatus* (Fig. 8.21)).

PHYLOGENETIC INTERPRETATION

(CH16) Ovipositor present - 0;

(CH17) hemisternites and sternites are united and divided - 2;

(CH18) tergite divided by membranous area - 1.

Scarabaeidae: Valginae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 6.38)

Ovipositor - present. Hemisternites and sternites - united and divided. Tergite - divided by a membranous area (e.g. Valginae sp. (Fig. 6.38)).

PHYLOGENETIC INTERPRETATION

(CH16) Ovipositor present - 0;

(CH17) hemisternites and sternites are united and divided - 2;

(CH18) tergite is divided by a membranous area - 1.

Scarabaeidae: Oncerinae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 8.22)

Ovipositor - present. Hemisternites and sternites - united and divided. Tergite - membranous (e.g. *Oncerus floralis* (Fig. 8.22)).

PHYLOGENETIC INTERPRETATION

(CH16) Ovipositor present - 0;

(CH17) hemisternites and sternites are united and divided - 2;

(CH18) tergite is membranous - 2.

Scarabaeidae: Chasmatopterinae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 6.40)

Ovipositor - present. Hemisternites and sternites - united; divided in two. Tergite - membranous bursa (e.g. *Chnaunanthus chapini* (Fig. 6.40)).

PHYLOGENETIC INTERPRETATION

(CH16) Ovipositor present - 0;

(CH17) hemisternites and sternites are united and divided - 2;

(CH18) tergite is membranous - 2.

Scarabaeidae: Orphninae

LITERATURE REVIEW

No literature available.

DESCRIPTION (FIG. 6.42)

Ovipositor - present. Hemisternites and sternites - united; divided in two. Tergite - divided by a membranous area (e.g. *Orphnus capensis* (Fig. 6.42)).

PHYLOGENETIC INTERPRETATION

(CH16) Ovipositor present - 0;

(CH17) hemisternites and sternites are united and divided - 2;

(CH18) tergite is divided - 1.

PLATE 37

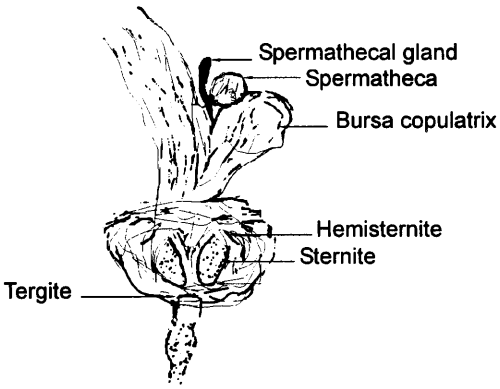


Fig. 8.1

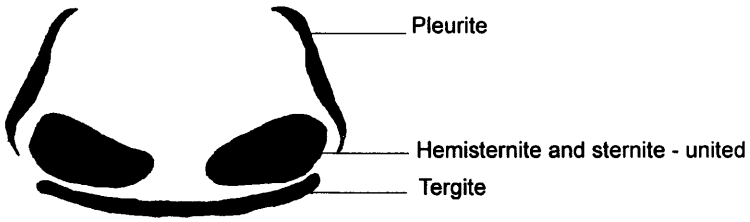


Fig. 8.2

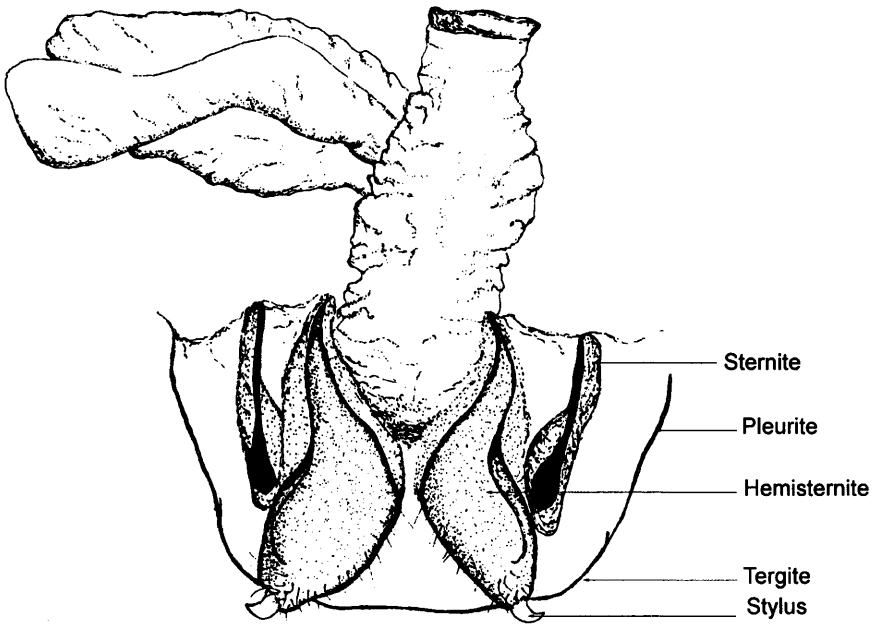


Fig. 8.3

Fig. 8.1 Ovipositor of a *Glaresis* species (Glaresidae)
Fig. 8.2 Ovipositor of *Odontotaenius disjunctus* (Passalidae)
Fig. 8.3 Ovipositor of a Lucanidae species an unidentified Lucanidae species
Drawings not to scale

PLATE 38

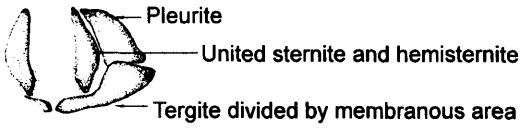


Fig. 8.4

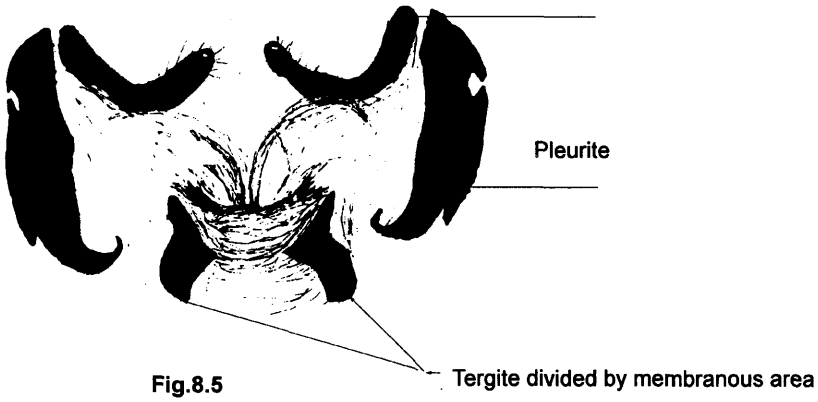


Fig.8.5

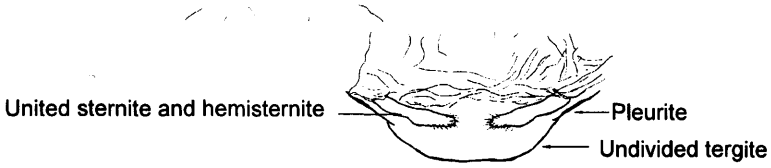


Fig.8.6

Fig. 8.4 Ovipositor of *Lichnanthe rathvoni* (Glaphyridae)
Fig.8.5 Ovipositor of *Omorgus asperulatus* (Trogidae)
Fig.8.6 Ovipositor of *Elephastomus meraldus* (Bolboceratidae)
Drawings not to scale

PLATE 39

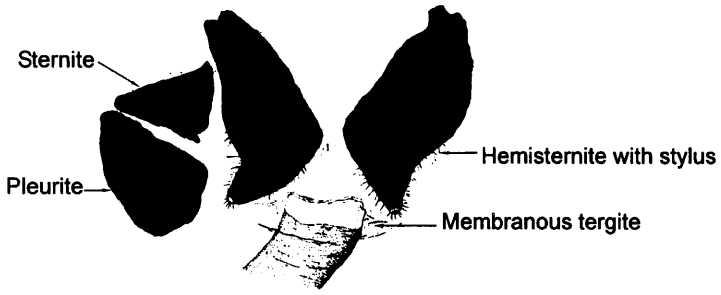


Fig. 8.7

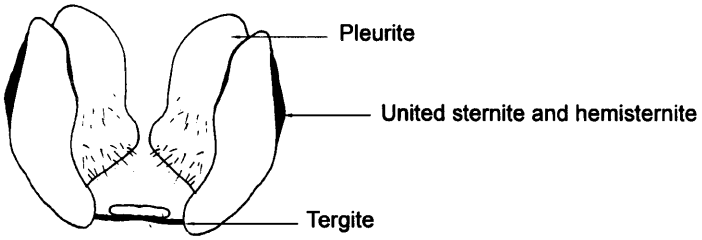


Fig. 8.8

Fig. 8.7 Ovipositor of *Pleocoma edwardsii* (Pleocomidae)
Fig. 8.8 Ovipositor of *Pleocoma dubitabilis* (Pleocomidae)
Drawings not to scale

PLATE 40

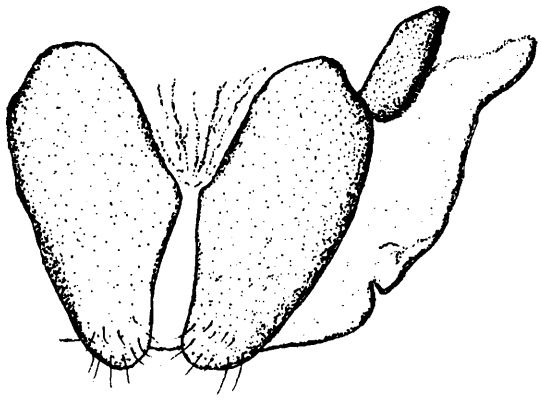


Fig. 8.9

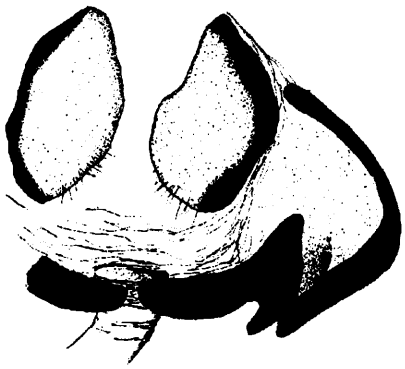


Fig. 8.10

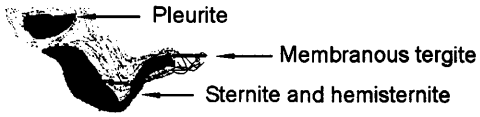


Fig. 8.11

Fig. 8.12

Fig. 8.13

Fig. 8.9 Ovipositor of *Lethrus apterus* (Geotrupudae)
Fig. 8.10 Ovipositor of *Frickius variolosus* (Geotrupidae)
Fig. 8.11 Ovipositor of *Ochodaeus inarmatus* (Ochodaeidae)
Fig. 8.12 Bursa, spermatheca, spermathecal gland and ovipositor of *Liparochrus hackeri* (Hybosoridae)
Fig. 8.13 Ovipositor of *Ataeinus cognatus* (Aphodiinae)
Drawings not to scale

PLATE 41

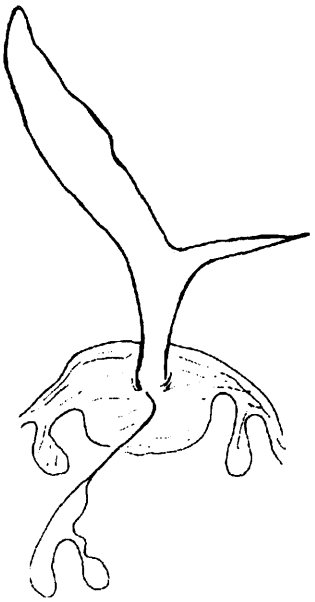


Fig. 8.14

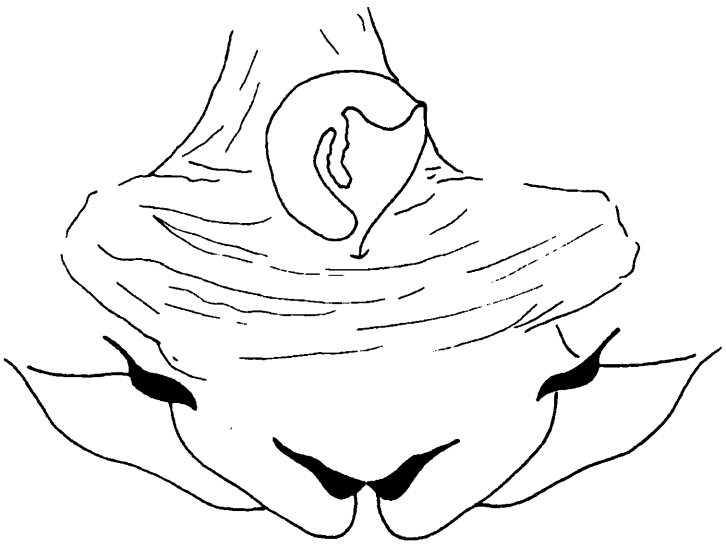


Fig. 8.15

Fig. 8.14 *Diastellopus thomsoni*, an example where the ovipositor is not present (Scarabaeinae)
Fig. 8.15 Ovipositor of *Proagoderus fossidorsis* (Scarabaeinae)
Drawings not to scale

PLATE 42

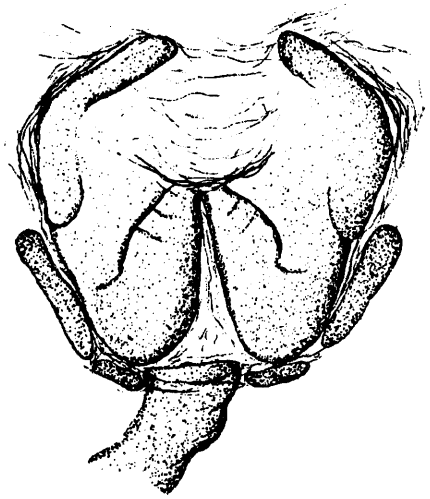


Fig. 8.16

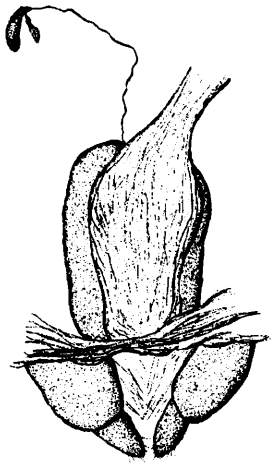


Fig. 8.17

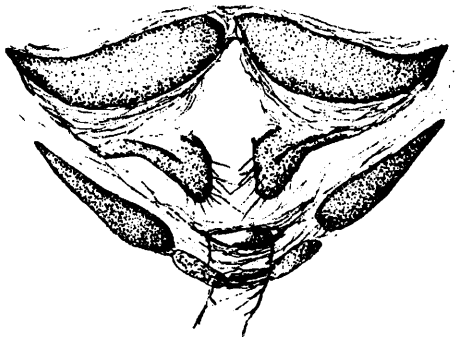


Fig. 8.18

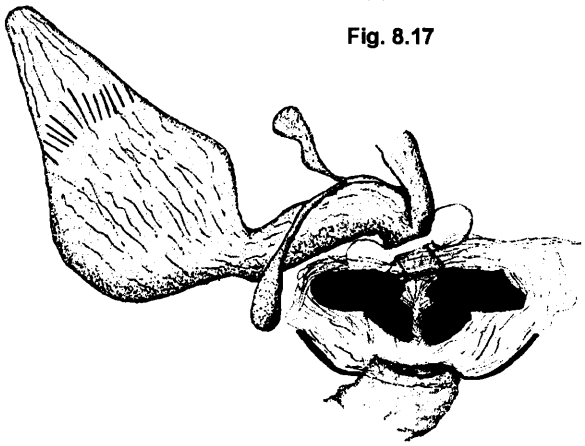


Fig. 8.19

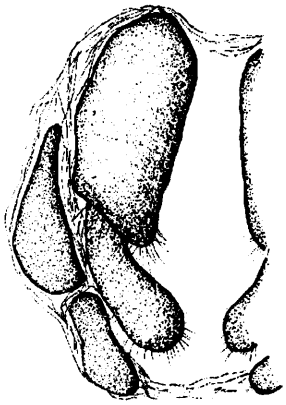


Fig. 8.20

Fig. 8.16 Ovipositor of *Schizonycha puncticollis* (Melolonthinae)
Fig. 8.17 Bursa, spermatheca, spermatheca gland and ovipositor of *Peritrichia subsquamosa* (Rutelinae)
Fig. 8.18 Ovipositor of an *Eriesthes* species (Hopliinae)
Fig. 8.19 Bursa, spermatheca, spermathecal gland, accessory glands and ovipositor of *Heteronychus arator* (Dynastinae)
Fig. 8.20 Ovipositor of *Lamaptera cinnamonea* (Cetoniinae)
Drawings not to scale

PLATE 43

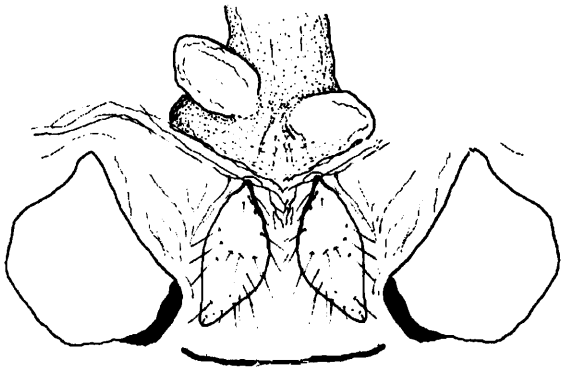


Fig. 8.21

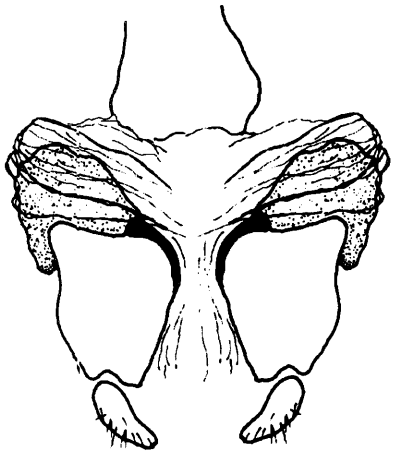


Fig. 8.22

Fig. 8.21 Ovipositor of *Campulipus limatus* (Trichiinae)
Fig. 8.22 Ovipositor of *Oncerus floralis* (Oncerinae)
Drawings not to scale

9. PHYLOGENY OF THE INTERNAL ORGANS AND OVIPOSITOR

Authors like Crowson (1938); Ritcher & Baker (1974); Holloway, (1972) and Iablokoff-Khnzorian, (1977) have suggested that the morphology of the internal organs and ovipositor might present important phylogenetic information. There are, however, authors who believe the internal organs and ovipositor are subjected to too much adaptation through the course of evolution, and that they are not usable in phylogenetic studies. One of the main reasons is that the morphology of these structures changes quickly and unpredictably when a "new" selection pressure is applied (Wiley, 1981; Caveney, 1986). The same selection pressure may also elicit different or random adaptive responses depending on the genotypic and phenotypic characteristics (Bock, 1965). In the past, authors (like those above and others) have speculated on the usefulness of the systems and I, earlier in this thesis, argued for the use of "adaptive characters" in phylogenetic analysis (see Introduction).

Hennig (1981) provided certain criteria when using morphological characters to imply phylogeny of a group. The criteria are the following:

- The studied species should belong to a monophyletic group.
- Irrespective of rank, every group formation in the phylogenetic system must be established by derived (apomorphic) characters in its groundplan.
- Where two monophyletic groups (sister groups) together form a monophyletic group, some characters should always appear in a more primitive state (called relative plesiomorph by Hennig, 1981) in one of the two groups.

These criteria were applied to the character states of the internal organs and ovipositor to see whether it is worthwhile to try to analyse the characters and their states phylogenetically.

All three of the above criteria were met; therefore the internal organs and ovipositor could theoretically be used in a phylogenetic analysis. In this thesis, I have, however, tried to address three additional questions:

- Are the internal organs and ovipositor useful characters for cladistic analysis?
- If they prove useful, does the resulting cladogram confirm or reject relationships indicated in the Browne & Scholtz (in press) cladogram?
- Are all the character states of the internal organs and the ovipositor characters present as the most primitive state in the Glaresidae?

Eighteen internal organ and ovipositor characters with their character states were identified (discussed in previous chapters). The characters and their states were compiled in a data set (Table 9.1) and cladistically analysed to predict the phylogeny of these organ structures.

TABLE 9.1: Character states of the 13 families of the Scarabaeoidea.

	CHARACTER NUMBERS																	
FAMILY NAMES	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**
Glaresidae	0	0	0	0	0	0	0	2	0	0	0	0	0	1	0	0	0	0
Passalidae	0	0	1	0	0	0	0	1	0	1	0	0	0	1	1	0	1	0
Lucanidae	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0
Diphyllostomatidae	?	?	?	?	?	?	?	?	0	?	0	0	0	?	?	0	2	0
Glaphyridae	?	?	?	?	?	?	?	?	0	0	0	0	0	?	?	0	1	1
Trogidae	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	1	1
Bolboceratidae	0	0	1	0	0	0	0	2	0	0	1	1	1	0	0	0	1	0
Pleocomidae	1	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
Geotrupidae	1	1	1	0	0	0	1	2	0	0	1	1	0	0	0	0	1	1
Ochodaeidae	?	?	?	?	?	?	?	?	0	0	0	0	1	?	?	0	0	0
Ceratocanthidae	1	0	1	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1
Hybosoridae	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1
Scarabaeidae	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1

Cladistics is the most powerful and widely used technique utilised to determine relationships among taxa. As mentioned in the introduction, many authors have contributed to the development of phylogenetics and cladistics. Cladistic and phylogenetic definitions created by Hennig (1950, 1981), Wiley (1981) and Mayr and Ashlock (1991) form the basis of this thesis. Cladistics (a numerical technique) is based on maximum parsimony (Sober, 1989). The aim of this method (maximum parsimony) is to "simplify" results. Methods for estimating trees under the maximum parsimony criterion equate simplicity with the explanation of attributes shared among taxa as due to their inheritance from a common ancestor (Sober, 1989). The parsimony method tests the assumption of homoplasy (convergence, parallelism and reversals), and therefore if the character states associated with the clusters are studied, places where homoplasy occurs, can be identified.

The parsimony method also operates by selecting trees that minimise the total tree length (or number of evolutionary steps) and at the same time, minimises the homoplasies (not necessarily meaning that it will be able to draw a tree that is totally free of homoplasies).

Because there are so many different options to choose from when embarking on a cladistic analysis, a brief explanation on the procedures used in this analysis will be given. As mentioned in previous chapters, the computer program PAUP/Mac version 3.1.2d5 (Swofford, 1985) was used to perform the analysis.

- All characters were ordered (Wagner), which represent a linear transformation series (PAUP assumes that the character proceeds progressively through the different states).
- Characters were initially not weighted.
- The data set was subjected to a branch-and-bound search (the algorithm used by this method finds all minimum length trees).
- No initial upper bound was provided (PAUP then calculates one via step-wise addition – a step-wise addition of taxa to the developing tree is performed until all the taxa have been connected).
- No topological constraints were enforced (a topological constraint restricts the set of trees obtained according to the constraint specifications).
- Branches having maximum length zero were collapsed to yield polytomies.

- The trees were rooted using the outgroup method, and Glaresidae chosen as outgroup to the rest of the families.
- Character state optimisation was chosen as accelerated transformation (the optimisation command allows the user to specify the method used to resolve ambiguity when optimising ordered or unordered characters). Accelerated transformation prefers reversals to parallelisms.
- The maximum number of trees was specified as 100 (but PAUP allows one to increase the number of trees when the specified number is reached).

The analysis resulted in 90 trees of length 25 and consistency index of 0.640, a homoplasy index of 0.360 and a retention index of 0.690. The consistency index (ci) isthe average fit of all characters to the tree, and it usually varies from 1.0 for a perfect fit to a value approaching zero for the poorest fit. The ci is, however, inflated by autapomorphies, which can take only the value of 1.0; thus a totally uninformative data set consisting of e.g. only autapomorphies could present a ci of 1.0. The homoplasy index and the ci together will always present the value of 1.0, and it is an indication of the amount of homoplasy (similarity due to independent evolutionary change, e.g. parallelism, reversal and convergence) in the data set. The retention index is very similar to the ci, but defined so that the highest possible value for any character is 1.0 and the lowest 0.0, and therefore removes bias due to autapomorphies.

Although only 18 characters were analysed, the ci is relatively high (although this could be because of autapomorphies) and the homoplasy index is relatively low, indicating possibly little independent evolutionary change. The analysis produced 90 trees. Ideally there should be one tree for the character set. Different options are available in order to decide which tree is the "best", but to make that decision different options are available.

The first option was to perform a strict consensus (on the 90 trees with 25 steps each) but the resulting tree possessed unresolved nodes (families Glaresidae, Passalidae, Lucanidae, Diphyllostomatidae, Pleocomidae and Ochodaeidae) (Fig. 9.1). Unresolved nodes (branching points) imply many relationships or combinations of the taxa involved.

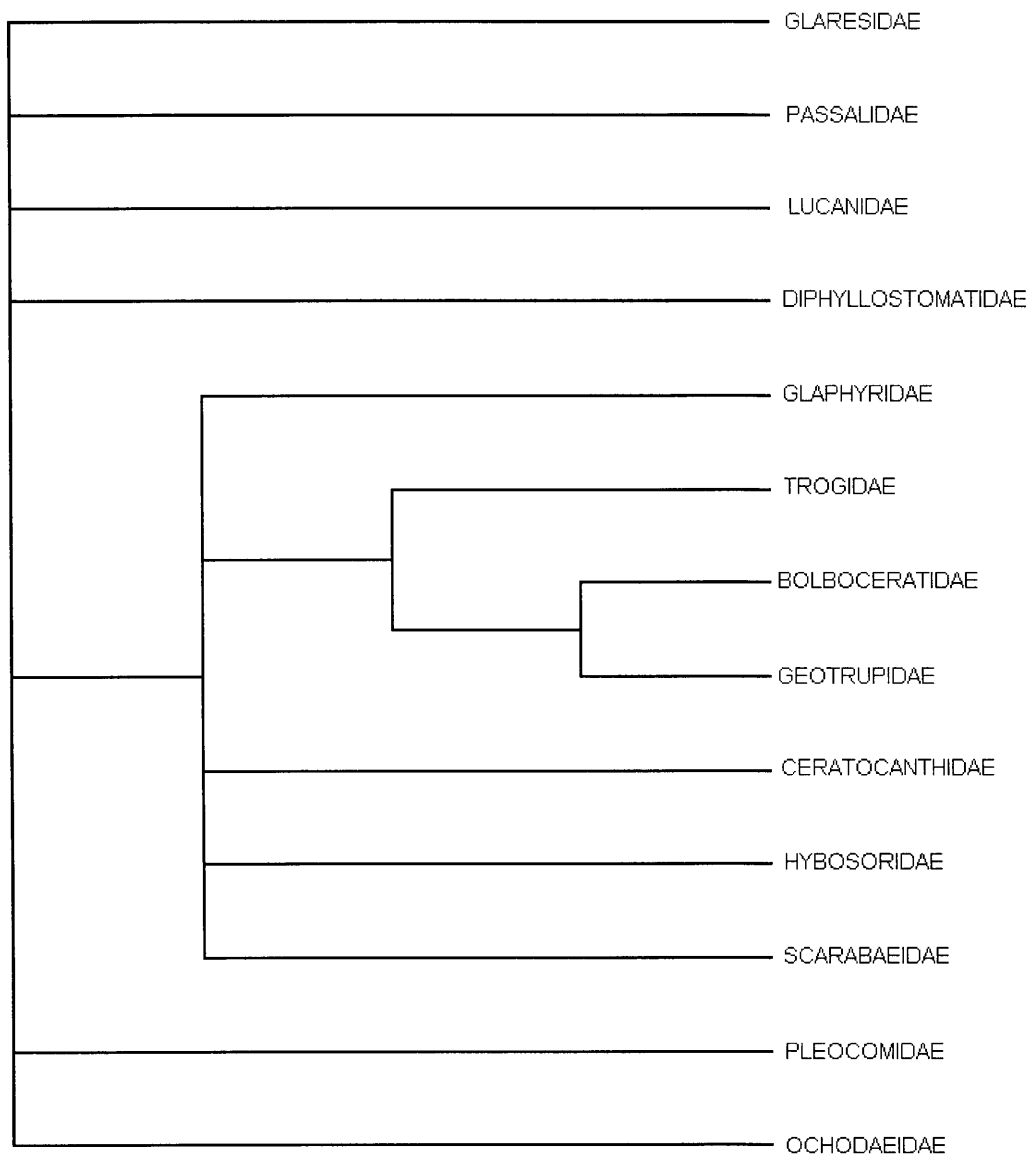


Fig. 9.1 Strict consensus tree (from 90 trees and 25 steps).

It was therefore decided to find the 50% majority rule consensus tree, again using all 18 characters (90 trees with 25 steps) (Fig. 9.2).

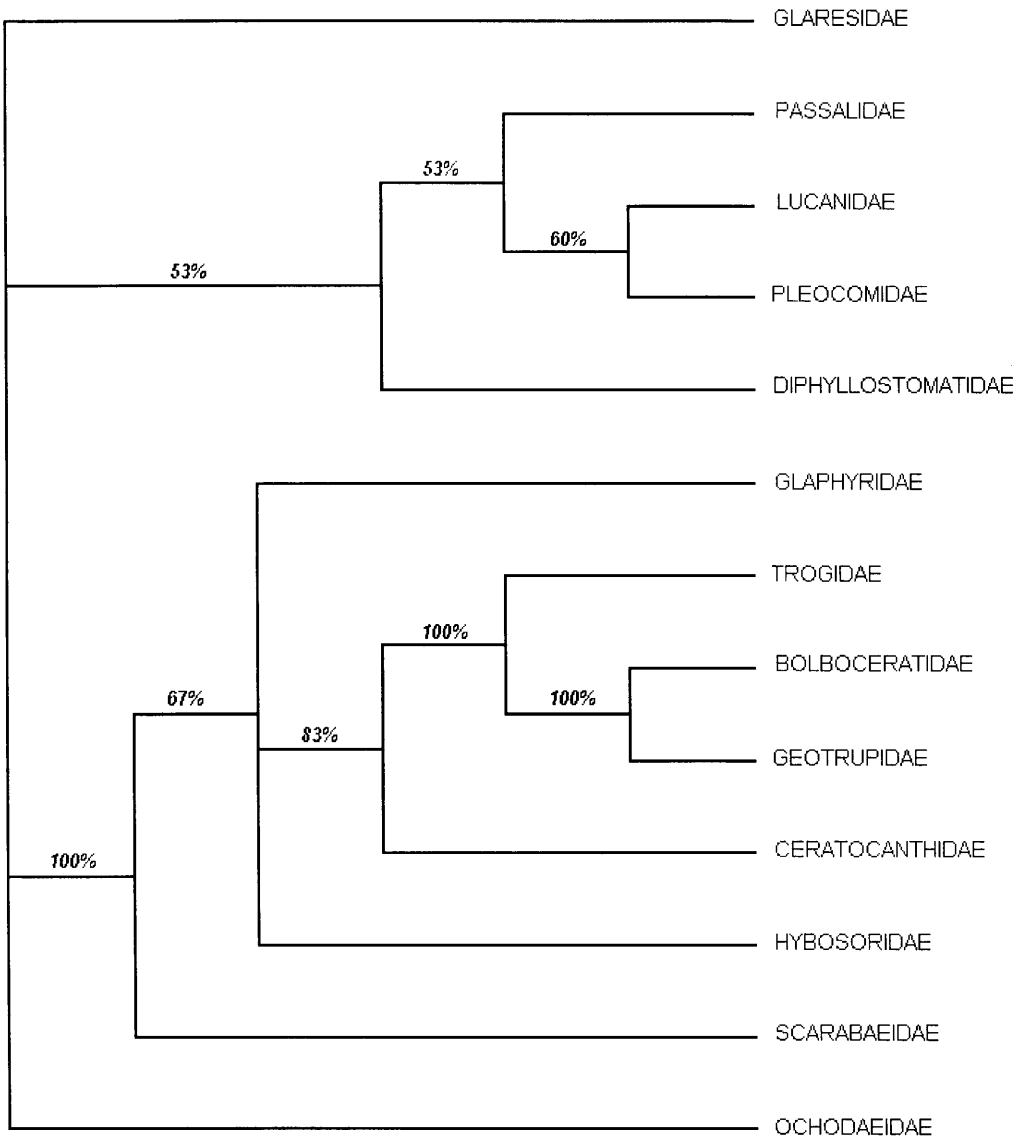


Fig. 9.2 The 50% majority rule consensus tree, using all 18 characters (from 90 trees and 25 steps).

This type of consensus tree is much more informative than the strict consensus as it finds the percentage value of each cluster (how many times each taxon is grouped in a specific cluster in the total number of trees). A value of 100% will be allocated to those taxa that are always clustered together (in all 90 parsimonious trees). A percentage between 70% and 100% is a relatively high clustering combination, but less than 50% does not have any

phylogenetic value, as the taxa in those clusters are not supported enough and there are too many other clustering combinations possible. There were no unresolved nodes in the 50% majority rule tree. The taxa that formed unresolved nodes in the strict consensus tree, were allocated very low clustering percentages in the 50% majority rule tree. Passalidae, Lucanidae, Pleocomidae and Diphyllostomatidae always grouped together 53% of the times. Within this cluster, Lucanidae and Pleocomidae grouped together 60% of the times, and Passalidae, Lucanidae and Pleocomidae grouped together 53% of the times. Glaphyridae, Trogidae, Bolboceratidae, Geotrupidae, Ceratocanthidae, Hybosoridae, and Scarabaeidae, however, grouped together 100% of the times. Within this cluster, Trogidae, Bolboceratidae, Geotrupidae and Ceratocanthidae were grouped together 83% of the times, while Trogidae, Bolboceratidae and Geotrupidae were grouped together 100% of the times. Within this cluster, Bolboceratidae and Geotrupidae were grouped together 100% of the times.

Because not all character states are judged to be parsimony-informative, they were weighted according to the consistency index. Weighting of characters, could, however, suggest that the researcher is intervening in the unbiased parsimony process. Weighting according to the consistency index, however, identified autapomorphies (diagnoses the terminal taxon where it is found, but uninformative about relationships to other terminals or taxa, and therefore useless for cladistic tree-building) and parsimony-uninformative constant character states (where e.g. character 1 only has one state (e.g. 0) for all the taxa) between the taxa. These character states do not present additional information about the relationships between taxa. The parsimony-informative characters are given weight according to the number of reversals and parallelisms/convergences involved. The less reversals and/or parallelisms/convergences, the higher the weight assigned (weights assigned and number of characters involved are shown in Table 9.2). There are 10 parsimony-informative characters. The parsimony-informative characters with a weight of 1 (characters 10, 11, 12 and 14) are the most informative characters. Table 9.3 shows which of the total 18 characters are informative and which uninformative.

They also present no reversals or parallelisms/convergences on the tree. The rest of the parsimony-informative characters possess indexes varying from 0.33 to 0.5 and 0.67. They all present reversals or parallelisms/convergences (each character discussed in detail later).

TABLE 9.2: Number of characters of the families of the Scarabaeoidea weighted according to the consistency index

NUMBER OF CHARACTERS	CHARACTER WEIGHT
12	1
2	0.333333
3	0.500000
1	0.666667
4	constant
4	parsimony-uninformative

TABLE 9.3: Parsimony-informative and uninformative characters. (- are informative characters; U are uninformative; UC are constant but uninformative).

CHARACTER	STATUS	WEIGHT	STATES
1	-	0.333333	01
2	U	1.000000	01
3	-	0.333333	01
4	UC	1.000000	0
5	U	1.000000	01
6	UC	1.000000	0
7	U	1.000000	01
8	-	0.500000	012
9	UC	1.000000	0
10	-	1.000000	01
11	-	1.000000	01
12	-	1.000000	01
13	-	0.500000	01
14	-	1.000000	01
15	U	1.000000	01
16	UC	1.000000	0
17	-	0.666667	012
18	-	0.500000	01

With the parsimony-uninformative characters removed (leaving 10 parsimony-informative characters), branch-and-bound search was again performed, this time resulting in 12 steps and 54 parsimonious trees.

Bootstrap (with the ten characters) and 500 replications (on the 54 trees and 12 steps) was also performed on the data set. This was, however, unsuccessful as the only relationship supported (and only 69% of the time) was between Geotrupidae and Bolboceratidae.

A 50% majority rule consensus was then performed on the 10 parsimony-informative characters (Fig. 9.3). The parsimony-informative characters and their state changes are plotted onto this tree.

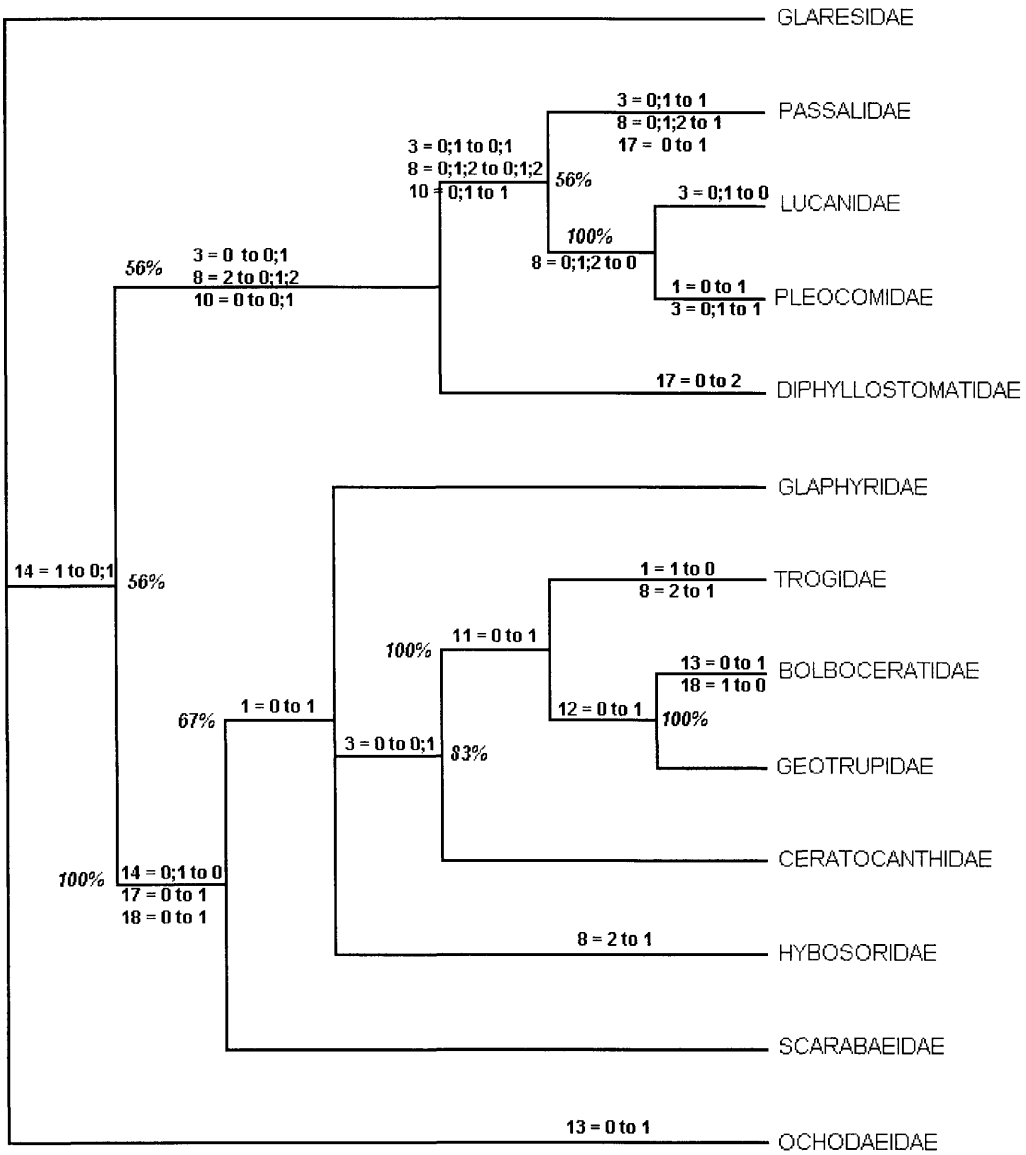


Fig. 9.3 The 50% majority rule consensus tree (from 54 parsimonious trees and 12 steps), showing the 10 parsimony-informative character state changes.

Instead of using the 50% majority rule consensus tree as representing the phylogeny, one could take all 54 trees and decide, based on criteria like character state changes, parallelisms and reversals, which tree provides the best indication of phylogeny. Authors like Brooks *et al.* (1986) and Carpenter (1988) suggested various methods to select such a tree but choosing the tree (using various criteria) can be biased, and since the philosophy behind cladistics is to be as unbiased as possible, I do not feel comfortable choosing a single tree. In the 50% majority tree all nodes were resolved, and from the percentages one can decide whether the clusters are informative or not.

The 50% majority rule tree presented the following two major clusters, the first consisting of Passalidae, Lucanidae, Pleocomidae and Diphyllostomatidae. This combination is supported 56% of the time. Within this cluster, the Lucanidae and Pleocomidae association is supported 100% of the time. The second cluster consisting of the Glaphyridae, Trogidae, Bolboceratidae, Geotrupidae, Ceratocanthidae, Hybosoridae and Scarabaeidae are constant 100% of the time. Within this cluster, Trogidae, Bolboceratidae and Geotrupidae are clustered together 100% of the time, with Bolboceratidae and Geotrupidae always forming a terminal cluster (this was also supported by the strict consensus (90 trees, 25 steps), 50% majority rule (90 trees, 25 steps) as well as bootstrap (54 trees, 12 steps).

The cluster Trogidae, Bolboceratidae, Geotrupidae and Ceratocanthidae was supported 83% of the times, also making this combination relatively strong. Hybosoridae and Glaphyridae do not cluster with any other taxa. Ochodaeidae appear in a cluster of its own.

PARSIMONY-INFORMATIVE CHARACTERS

The parsimony-informative characters and their state changes were plotted onto the tree (Fig. 9.3). The different characters and their state changes are mentioned in the following paragraphs.

Character 1: Length of the midgut:

This character is found in both major clusters and has developed parallel or convergently. In cluster 1 the state changes from 0 to 1 (Lucanidae). In cluster 2 it changes from 0 to 1 early in the cluster with Scarabaeidae retaining the 0 state. It, however, undergoes a reversal (from 1 to 0) in the Trogidae.

Character 3: Regions of the midgut:

Found in both clusters 1 and 2. In cluster 1 both states (0 and 1) are found. No reversals take place.

Character 8: Number of abdominal ganglia:

Because Glaresidae was chosen as the outgroup for the data set, its state (2) was taken by PAUP as most plesiomorphic and therefore character 8 is presumed to go from 2 to 0 to 1.

The character state 0 is present in the Lucanidae and Pleocomidae and changes to 1 in the Diphyllostomatidae. In the second cluster, it stays 2 (the chosen plesiomorphic state) but in the Hybosoridae it goes to 1. No reversals are present, only parallel or convergent character state changes.

Character 10: Number of ovarioles:

This a stable character as the character state stays the same in the second cluster, (as 0) and varies from 0 to 1 in the first cluster. No reversal or parallel/convergent character state changes take place.

Character 11: Form of the bursa copulatrix:

This character stays in the plesiomorphic state in the first cluster. In the second cluster it changes from 0 to 1 and the apomorphic state is present in Geotrupidae, Bolboceratidae and Trogidae. No reversal or parallel/convergent character state changes take place.

Character 12: Presence of glandular structures:

This character stays in the plesiomorphic state in the first cluster. In the second cluster the character state changes from plesiomorphic to apomorphic only in the Geotrupidae and Bolboceratidae. No reversal or parallel/convergent character state changes take place.

Character 13: Attachment of spermathecal duct:

This character stays in the plesiomorphic state in the first cluster. The character stays in the plesiomorphic state in the second cluster except in Bolboceratidae where it goes from 0 to 1. Ochodaeidae also possess character state 1. No reversals take place. The change from 0 to 1 in Ochodaeidae and Bolboceratidae suggests parallel or convergent character state change.

Character 14: Number of testicular lobes:

Because Glaresidae is chosen as the outgroup for the data set, its state (1) was taken by PAUP as the plesiomorphic state and therefore character 14 is presumed to go from 1 to 0. This character is 0 in the first cluster and second cluster. In the Ochodaeidae character state 1 is present. No reversal or parallel/convergent character state changes take place.

Character 17: Presence of hemisternites and sternites:

In the first cluster, character state 1 is present in Passalidae and 2 is present in Diphyllostomatidae. The rest of the families possess the plesiomorphic state. The character state change from 0 to 1 appears early in the second cluster. No reversal or parallel/convergent character state changes take place.

Character 18: Form of tergite:

The plesiomorphic state is present in all taxa of the first cluster. Th apomorphic state is present in all taxa of the second cluster except in the Bolboceratidae where the 0 state is found – representing a reversal.

PARSIMONY-UNINFORMATIVE INCONSTANT CHARACTERS

Although these characters are not informative, they possess plesiomorphic as well as apomorphic character states, but the apomorphic state only appears in one taxon (representing an autapomorphy).

Character 2: Length of midgut:

Missing data are present, and character change 0 to 1 only appears in the Geotrupidae, presenting an autapomorphic character state.

Character 5: Different characters of the hindgut:

Missing data are present, and character change 0 to 1 only appears in the Lucanidae (autapomorphy).

Character 7: Number of thoracic ganglia present:

Missing data are present, and character change 0 to 1 only appears in the Geotrupidae (autapomorphy).

Character 15: Number of accessory glands:

Missing data are present, and character change 0 to 1 only appears in the Passalidae (autapomorphy).

PARSIMONY-UNINFORMATIVE CONSTANT CHARACTERS

Characters 4 (Attachments of the Malphigian tubules), 6 (position of the suboesophagial ganglion) 9 (number of ovaries) and 16 (presence of an ovipositor) all have missing data and where data were available, only the plesiomorphic state was present.

With the cladistic analysis complete, the three questions posed in the beginning of the chapter can now be addressed individually:

Can we use the internal organs and ovipositor characters in a cladistic analysis?

According to Hennig's criteria the answer is yes. We, however, need to provide statistical backing. Hills & Huelsenbeck (1992) provide a table to determine signal, noise, and reliability in molecular phylogenetic analysis (although this is aimed at molecular work, character state changes (presented as binary data) are evaluated and not the characters itself). The aim is to determine how the data set is faring compared to any random set of character states. PAUP provides a GI rating for the data and this is compared to tables provided by the authors. According to the table, the internal organs and ovipositor are rated at the 95% level, suggesting that they are suitable for cladistic analysis.

Another problem could possibly be the small number of usable characters. The real test, however, is how the cladogram produced from the data set, compares to that of the large variable data set analysed by Browne & Scholtz (in press).

In other words, does the resulting cladogram confirm or reject the placements of the taxa in the Browne & Scholtz (in press) cladogram?

The Browne and Scholtz cladistic analysis indicated two basal lineages; the glaresid lineage and a second lineage that is divided into two lower level lineages, the passalid and scarabaeid lineages. The passalid lineage contains two lines, the glaphyrid and geotrupid line. The glaphyrid line contains Passalidae, Lucanidae, Diphyllostomatidae, Trogidae, Bolboceratidae, Pleocomidae and Glaphyridae. The geotrupid line of the cladogram contains Geotrupidae, Ochodaeidae, Ceratocanthidae and Hybosoridae.

The two main clusters of the internal organ tree differ slightly from the two lines of the passalid lineage of the Browne and Scholtz tree, and my main concern is the placement of

the Scarabaeidae together with the second lineage in the internal organ tree and the fact that the Ochodaeidae is placed on its own and outside the two main clusters. In the internal organ tree, Bolboceratidae and Geotrupidae clustered together in a terminal cluster (100% of the times), where they occur in separate lines in the Browne and Scholtz tree.

Glaphyridae and Trogidae also appear in the first cluster (the more primitive taxa) of the organ tree but in the glaphyrid line (together with the more derived taxa) of the Browne and Scholtz tree.

The Geotrupidae and Bolboceratidae association in the organ tree can now be inspected a little more closely. The Geotrupidae were previously divided into the Geotrupinae, Bolboceratinae, Taurocerastinae and the Lethrinae. These subfamilies were traditionally united mainly by the fact that most of the taxa have 11-segmented antennae (except Taurocerastinae – 10-segmented antennae). Howden (1982) treated the Geotrupidae as a subfamily of the Scarabaeidae (with Bolboceratidae as a tribe (Bolboceratini) included in his Geotrupinae) and based the grouping on two synapomorphic attributes, detritus-feeding and provisioning of larval burrows by adults.

Various early studies e.g. Scholtz (1990); Browne (1991a, 1993) and Scholtz *et al.* (1994), however, suggested that the Geotrupidae is probably polyphyletic because there are two distinct and apparently unrelated groups identifiable in the family (the Bolboceratinae group and the Geotrupinae, Lethrinae and Taurocerastinae group). In 1996, Browne & Scholtz, based on a review of 30 phylogenetic important adult and larval characters, suggested that the Bolboceratinae is monophyletic (as the taxon does not share any demonstrable apomorphs with any other member of the Geotrupidae or with any other taxon of the Scarabaeoidea). Because it did not fit into any existing groups, Bolboceratidae was accorded family status.

The organ tree, however, suggests that the two families are phylogenetically extremely close and they share all character states except those of characters 13 (attachment of spermathecal duct) and 18 (form of the tergite). The Geotrupidae possess the plesiomorphic state of character 13 and the apomorphic state of character 18. Bolboceratidae possess the

apomorphic state of character 13 and character 18 possibly underwent a reversal back to the plesiomorphic state.

Bootstrap (500 replications) indicated only one resolved node (with Bolboceratidae and Geotrupidae), and both the weighted and unweighted 50% majority rule consensus trees placed them together 100% of the times. Although Browne & Scholtz (1996) provided very good explanations why members of the Geotrupidae and Bolboceratidae should be placed in two different families, this is not reflected in the internal organ and ovipositor characters.

Although very few characters were analysed and proved to be parsimony-informative, overall the organs tree does not vary too much from the Browne & Scholtz tree. The answer to the question is therefore: although there are differences (especially pertaining to Bolboceratidae and Geotrupidae), the placements do echo the broad trends in the Browne & Scholtz tree.

The final question is: Can we confirm or reject the hypothesis that Glaresidae is the most primitive living scarabaeoid and sistergroup of the rest of the superfamily as proposed by Scholtz *et al.* (1996)?

Because Scholtz *et al.* (1996) identified Glaresidae as the most primitive living scarabaeoid and sistergroup of the rest of the Scarabaeoidea, in the present cladistic analysis, Glaresidae was chosen to root the cladogram, and therefore automatically placed outside the rest of the taxa (accepted by PAUP as the monophyletic group).

The character states of Glaresidae are all plesiomorphic, except characters 8 (number of visible abdominal ganglia) and 14 (number of testicular lobes).

Character 8 - Number of visible abdominal ganglia

The number of visible abdominal ganglia is a very stable character and the character states are:

Three ordered character states: plesiotypic state 0 - all six ganglia visible, first one or two abdominal ganglia fused to metathoracic ganglion; all other abdominal ganglia connected to each other with relatively long connectives; Apotypic state 1 - abdominal ganglia separately visible but connectives absent, the only distinction between ganglia is small holes; the first

abdominal ganglion - fused to the metathoracic ganglion; Apotypic state 2 - abdominal ganglia all fused to one another and to the metathoracic ganglion.

The derived apotypic state 2 is present in Glaresidae (all abdominal ganglia fused to the metathoracic ganglion). The reason why the derived condition is present in members of the Glaresidae is either because the beetles are very small, there is not enough space for long connectives, forcing ganglia to move closer to each other, or because of parallelism or convergence.

Character 14 - Number of testicular lobes

The number of testicular lobes is not a very reliable character, as it varies even between members of the closely related Scarabaeoidea taxa, Six was, however, considered the primitive number in the superfamily. This was decided because, for females, six is the primitive number of ovarioles per side (Ritcher & Baker, 1977 and Scholtz, 1990) and the number of ovarioles and number of testicular lobes usually correlate (except in the Glaresidae and the Scarabaeinae). The two unordered character states were: plesiotypic state 0 - six testicular lobes per side; apotypic state 1 – more or less than six testicular lobes per side. Because of the great variability of the number of testicular lobes, even between closely related taxa, only one apomorphic state was decided upon.

Glaresidae possess 4 testicular lobes per side (an apomorphy). The apomorphy could be the result of the following: an autapomorphy, a convergency/parallelism, a reduction or a reversal. Another option is that in fact, four is the primitive number of testicular lobes.

An autapomorphy is ruled out, because four testicular lobes per side are also present in some members of the Aphodiinae. Males of e.g. *Pinotus carolinus* (Aphodiinae) possess four testicular lobes per side (Williams, 1945). This can either present a parallelism/convergency, or a reduction (from six to four) or reversal back to the Glaresidae number. A reduction of the number of testicular lobes in Glaresidae could have taken place, although going from six to four is probably more difficult that going from six to three.

The number of testicular lobes, may also have been inherited either as a reversal or fouras the primitive number of lobes from the outgroup of the superfamily. If the character state for

six testicular lobes is present in the outgroup, but there are members of the outgroup possessing four testicular lobes, this can represent a reversal in Glaresidae, back to the four testicular lobes character state. If four is the plesiomorphic character state for the Scarabaeoidea, the character state for four testicular lobes could be present in the outgroup, and inherited unchanged by Glaresidae.

Although two possibly apomorphic character states are present in the Glaresidae, I do believe that the character states of the internal organs and the ovipositor indicate that Glaresidae is the most primitive living scarabaeoid.

My final conclusion is that the internal organs and ovipositor should not be neglected in phylogenetic studies. I believe that the informative characters should be included in the large database of morphological characters already existing for the Scarabaeoidea. Without these characters, the database is incomplete. Concerning the concept of adaptation and the belief that internal organs are adaptations and therefore useless in phylogeny: I do not agree.

SECTION 2

Geometric morphometric analysis of the metendosternites of the Scarabaeoidea

10. GEOMETRIC MORPHOMETRIC ANALYSIS OF THE METENDOSTERNITES OF THE SCARABAEOIDEA

Introduction

The metendosternite (also known as a furca) is chitinous and situated at the margin of the thorax and abdomen. It is a forked endosternal process of higher pterygote insects, formed by the sternal apophyses (also called the furcal arms) supported on a median inflection of the sternum (ventral wall of the thoracic segments) of the insect- these sternal apophyses become the prongs of the forked metendosternite (Snodgrass, 1935). The outer ends of the sternal apophyses are closely associated with the inner ends of the pleural arms. The metendosternite provides attachments for the inter-segmental longitudinal muscles, gives attachment to some ventral muscles of the legs, as well as giving attachment for specific muscles of the segments (Crowson, 1981).

In beetles, the metendosternite displays considerable diversity of structure and may be of great systematic importance Crowson (1981). Of the different forms, the Cupedid metendosternite is believed to be the ancestral type for the Coleoptera (Crowson, 1938). On the other hand, the Hylocoetoid furca is considered a modification of the Cupedid type, and the ancestral form to many of the members of the Polyphaga (Crowson, 1938, 1944).

In primitive beetles, the metasternum bears a transverse suture which divides the sternum into two parts (the anterior basisternum and the posterior furcisternum) and a median, longitudinal suture. The metendosternite is borne on the furcisternum and has a stalk that originates from the middle of the furcisternum and has a ventral median flange, which is basally continuous with the dorsal ridge of the longitudinal suture of the sternum. Anteriorly, the stalk broadens and is at its widest above the sternal suture where it bears a ventral transverse flange or ventral process (Crowson, 1944). The junction between the ventral process and the stalk forms a crux, the anterior part of which narrows into the median projection that may end near the level of the front margin of the metasternum.

The Hylocoetoid differs from the Cupedoid type, mainly in the structure of the crux. According to Crowson (1944), the Hylocoetoid metendosternite evolved from a dascillid-like

type of metendosternite which does not possess distinct furcal arms, but derived lateral parts of the ventral process that are differentiated from the narrow central part.

The metendosternite of Scarabaeoidea consists of a stalk, varying in length from short (only found in the Passalidae) to long (Scarabaeinae and Melolonthinae). The ventral transverse flange varies from a narrow, curved structure (Passalidae) to a strongly developed structure (Melolonthinae). The median projection varies from a strongly developed, anteriorly projecting structure (Passalidae) to a ventrally curved structure (Aphodiinae). A ventral rib, not visible dorsally, varies from a flattened (Scarabaeinae) to a broadened structure (Valginae and Melolonthinae) (Iablokoff-Khnzorian, 1977).

Except for authors like Crowson (1938; 1944; 1981) and Iablokoff-Khnzorian (1977) who superficially discussed the metendosternite structure of the Scarabaeoidea, no comprehensive treatment of the metendosternite of the Scarabaeoidea has ever been considered. Crowson (1938 and 1944), who examined the metendosternite of approximately 450 genera of Coleoptera, including 14 species of Scarabaeoidea, suggested that the diversity in structure of the metendosternite may potentially be of great taxonomic importance, particularly because it is apparently monophyletic in origin (as its origin can by traced to the primitive Hylecoetoid furca). Crowson (1938) based his conclusion that the metendosternite origin is monophyletic on evidence from his study of the Coleoptera genera, as well as information he considered corroborative as presented by various authors, e.g. the larval system of Böving & Craighead (1931). Based on the structure of the metendosternite, Crowson tentatively placed the taxa that he studied in a phylogenetic sequence.

Consequently, the present chapter represents the first comprehensive analysis of the metendosternite in the Scarabaeoidea using geometric morphometrics, a technique considered very effective for capturing differences in shape.

The development of Geometric Morphometrics: an overview

Biologists have long been interested in the shape and size of organisms, and to devise ways to compare size and shape differences amongst the organisms they are studying. Presently, some biologists are using a technique called geometric morphometrics to analyse and compare size and shape differences. The field of morphometrics is concerned with methods

for the description and statistical analysis of shape variation within and among samples of organisms and of the analysis of shape change as a result of growth, experimental treatment and evolution (Rohlf & Marcus, 1993).

An overview of different techniques (to compare shape and size differences amongst biological specimens) leading to the development of geometric morphometrics, follows. All the techniques discussed influenced developers of modern day geometric morphometrics.

One of the first researchers to explore the possibility to devise a quantifiable method by which shape could be examined was Thompson in 1917. He used a transformation grid that depicts the overall form of one organism as a distortion in shape of another organism (referred to as a reference organism). The idea was to place a Cartesian co-ordinate grid over the reference organism and then distort the image of the organism (including the grid) in various ways until the form of the second organism was achieved. The differences in shapes of the two organisms are then shown by the deviations of the fitted grid from the original simple squared grid. Over recent years, attempts have been made at providing Thompson's grids with a sound mathematical framework, and to adjust his original concept.

Huxley (1932) analysed differential growth relationships (allometric growth) between organisms. He measured either the size or weight of an organism and called it (x) and the size (or weight) of the differentially growing organ (y) and then determined the relationship between x and y. Huxley studied the growth relationships of a number of organisms including that of the crab *Carcinus maenas* where negative allometric relationships were explored. One of Huxley's important conclusions was that animals would preserve their shape unchanged, with increased size, if all organs are growing at the same rate. This phenomenon is referred to as isometric growth.

Since Huxley proposed his allometric equation, many researchers have tried to improve the technique. Blackith (1965) proposed a solution, which uses multivariate regression. Jolicoeur (1963) developed a method based on principal components, which assumes that the relative growth rates of all dimensions considered are constant. Kuhry & Marcus (1977) used bivariate linear models with the emphasis on the estimation of parameters in the bivariate linear representation of differential growth.

Many of the earlier methods of quantifying size and shape were rather *ad hoc*. Mosimann (1970) was one of the first researchers who tried to find a general solution for the problems quantifying size and shape. He was the first to use the terms shape vector and size variables. If two individuals have the same shape, then every shape vector of the first is equal to the corresponding shape vector of the second. Mosimann also proved that if any shape vector is independent of a particular size variable, then, in particular, the vector of proportions is independent of the variable. Isometry can therefore be defined as independence between a shape vector and a given size variable. Mosimann's approach to the analysis of size and shape played a fundamental role in the development of geometric morphometrics, as we know it today.

Over the last few years, methods have been developed to study the shape of an organism based on quantifying variation in the outline of the organism. Fourier analysis was one of the first methods to use this concept. The analysis is based on a mathematical theorem established by Baren Joseph Fourier (1768 - 1830). According to his theorem, every curve (no matter what its nature) can be exactly reproduced by superimposing a sufficient number of simple harmonic curves. This type of mathematics is known as Harmonic Analysis.

Rohlf & Archie (1984) used Fourier analysis to study similarities and differences in the outline of the wing-shape of mosquitoes. They noted, however, that the method employed dealt with overall shape variability only and not with changes in distance between homologous points.

The different models and techniques described in the previous paragraphs can be grouped under the heading multivariate morphometrics. This term was first introduced by Blackith & Reyment (1971). To sum up the meaning of multivariate morphometrics: it is the application of multivariate statistical analysis in biological variability in morphological characters, and not only shape variation.

Recently a different way of analysing variability in size and shape has emerged. This new school bases its methods on Thompson (1917) who used Cartesian co-ordinates to describe shape relationships between organisms. One of the most renowned researchers in geometric morphometrics is Bookstein (1978, 1990, 1991). In order to understand the basic

terminology and its uses in geometric morphometrics, the concepts behind the new concept of geometric morphometrics are explained in the following paragraphs.

The aspects of shape that usually contain as much information about the shape as possible are used. Form can be defined by two kinds of data, distances and co-ordinates (Fink, 1990). Distances are used more often, and are the quantitative descriptions of the length or size of an object. Co-ordinate data represent points on a grid, and are depicted as x and y co-ordinates. Co-ordinate data can be converted into distance data but distance data cannot always be converted into co-ordinate data. Bookstein *et al.* (1985), Bookstein (1991) and Zelditch *et al.* (1992) have criticised the traditional statistical analyses of distance measurements because of their inability to capture the spatial organisation Thompson (1917) intended to illustrate.

Shape can be defined as the outline of an object, which, in a two-dimensional space is a closed curve and in a three-dimensional space a surface. Biological specimens however, do not always have smooth surfaces, but ribs or bulges sometimes disturb the smoothness of the outline. Bookstein (1978) borrowed a term from craniometrics, called landmark, to label these features or special points on the outline of a biological specimen. To link biological and biometrical terms, homology is considered in geometric morphometrics as a mapping function, relating points to points on different organisms. A landmark should be homologous in all specimens studied, in order to compare the specimens with each other. A database of morphometric inquiry is therefore presented by samples of discrete points that correspond among all the forms of the data set. Landmarks, however, do not define the form of any edge or surface, they merely provide fixed points of reference on it. A morphometric analysis of outline data is therefore based on the assumption that a particular curve in one specimen corresponds to particular curves on all other specimens used in the data set. For the analysis to be interpreted in terms of homology, it is therefore essentialthat we know that certain points (landmarks) on a specific curve or outline match from one specimen to another (Bookstein 1990).

Bookstein (1978) formulated a formal definition of shape as the outline of landmarks from which all information about position, scale, and orientation has been drained. A change of shape is therefore a map of one shape on to another which sends arcs (or patches of

surface) smoothly on to arcs and corners or edges on to corners - therefore landmarks onto landmarks.

The main purpose of this new approach to geometric morphometrics is to permit description of variability as deformation and variability of deformation in a common geometric context. After the basic concepts about geometric morphometrics were developed by Bookstein, different researchers elaborated and refined the technique.

The following points characterise the new approach:
Data are recorded to capture the geometry of the structure being studied. This is in the form of two-dimensional or three-dimensional co-ordinates of morphological landmarks. Emphasis is given to recording homologous landmarks. Rather than just reporting that the shape has changed, one can report that certain structures have moved relative to others. If the overall outline of a structure or its surface is important, it can be captured by a sequence of digitised points along the outline or over the surface.

The geometrical relationships among the landmarks are not inherent in the raw co-ordinates themselves. The relationship among the points is captured by fitting an appropriate function to them in 2- or 3-D. The estimates of the parameters of the fitted function can then be used as variables in standard univariate and multivariate statistical analysis.

Siegel & Benson (1982) proposed a method for comparing configurations of landmarks on specimens of phylogenetically interesting genera of ostracods. This procedure is known as Procrustes superimposition (also used by Bookstein, 1991 and Rohlf & Slice, 1990). The method relies on a simple fit that expresses the differences between two organisms, and takes into account global parameters such as rotation, translation and scale of the structure under investigation. The method therefore superimposes chosen landmarks of one organism on top of the corresponding landmarks of the second organism in such a manner so as to minimise some measure of net discrepancy between homologues (the homologous landmarks of the two organisms therefore are matched as closely as possible according to an optimality criterion). Differences in shape are then expressed by disagreements in position of corresponding landmarks. Differences in shape are then reported in terms of residuals, usually shown graphically as displacement vectors at each landmark. The

residuals arising can then be used for studying contrasts in shape.

Another method used and developed by Bookstein (1978) is biorthogonal grids. This type of grid represents growth as two strains. Growth is portrayed as a symmetric tensor field over one whole image that can be compared with others on the same image. This technique has been largely surpassed by that of thin-plate splines and principal warps (Bookstein, 1991).

An important feature that morphometricians have been interested in, was to find away of carrying out the kind of shape studies inherent in the Thompson's grids, but for which no implicit structures for computing were provided. Bookstein (1989) developed methods that can do just that and this he called thin-plate splines and principal warps.

The term thin-plate spline comes from a model of the deformation of a thin metal sheet. The use of this spline does not imply that biological tissue behaves like metal sheets. It is simply a convenient function that is able to express the differences in two configurations of landmarks as a continuous deformation. These properties enable the automatic construction of transformation grids such as those associated with Thompson (1917). An important feature of this transformation is that one can separate those changes due to differences in size, translation, rotation and uniform shape changes (affine transformation) and those describing inhomogeneous changes (non-affine or local deformations). The purely inhomogeneous changes can further be split into principal warps - geometrically orthogonal components corresponding to deformations at different geometric scales.

In using thin-plate spines and principal warps, all landmarks are displaced by multiples of a single vector. To any transformation of landmarks there is a bending energy which is the net energy required to bend an infinite, infinitely thin metal plate over a set of landmarks so that its height over each landmark is equal to first the x-co-ordinate and the y-co-ordinate of the corresponding landmark in another set of landmarks. Any single non-uniform transformation may be expressed as a finite sum of principal warps, which are characteristic functions of the bending energy corresponding to Procrustean orthogonal displacements of the conceptual metal plate at the landmarks. These warps emerge in descending order of a latent root; bending energy per unit summed squared Procrustean displacement that is an inverse geometrical scale. The sum of the products over the landmarks of the displacements

in any particular direction is zero. Procrustean distance is the sum of the squares of these displacements. Needless to say the mathematical details of principal warps are quite complicated, and I refer the reader to Bookstein (1989a and 1990).

Relative warp analysis was developed from the thin-plate splines and principal warps. This analysis finds the thin-plate spline transformations that map a reference configuration of landmarks (usually the mean sample) onto each specimen.

Studies that have used geometric morphometrics as a tool, mostly analysed the shape variation of rigid anatomical structures such as skulls of closely related or morphologically similar species. Bookstein (1991) gave a detailed presentation of the mathematical basisfor relative warp analysis of within-population morphometric variation based on landmark data, and used cranial growth in rats and the analysis of Apert's syndrome in humans (a craniofacial anomaly) as examples.

One of the early examples of the use of geometric morphometrics as a tool in natural history studies was the analysis of 18 landmarks corresponding to points at which wing veins either branch or intersect the margin of the wings of eight species of *Anopheles* mosquitoes using Procrustes methods for optimal superimposition of landmarks (Rohlf & Slice, 1990). Rohlf later (1993b) re-analysed the landmark data from Rohlf & Slice (1990) using the relative warp analysis method of Bookstein (1991). The paper provides an alternative use for Bookstein's (1991) method and the aim was to make the technique more appropriate for natural history studies and to suggest new graphics techniques for representing the results of a relative warp analysis. The method of relative warps consists of fitting an interpolating function, the thin-plate spline of Bookstein (1989a) to the x, y co-ordinates of the landmark for each specimen in the sample. The relationships between relative warp analysis and canonical variates, Fourier analysis and Procrustes analysis were also discussed. This paper therefore added new techniques to expand geometric morphometric analysis.

The development and expansion of the terminology and work methods of geometric morphometrics encouraged authors to explore the usefulness of the results when comparing morphologically closely related species. Authors like Swiderski (1993), Fink & Zelditch (1995) and Rohlf *et al.* (1996) were some of the early workers who took the initiative to

analyse the morphology of closely related species by using geometric morphometrics.

Swiderski (1993) analysed the morphology of the scapula in 16 species of tree squirrels, chipmunks and ground squirrels (Scuiridae). The aim of the study was to determine whether the scapula evolved as an integrated unit, or as a collection of distinct parts. Scapular shape among species was analysed by thin-plate splines, and principal warps and partial warps were used to describe differences between the species in the study group. In the analysis, the 16 species were compared with one starting form that was considered as representing the ancestral morphology of the study group. The mean scapular shape of the tree squirrels was therefore used by the author as a reference shape and this was thought to approximate the ancestral shape. There are two main issues confused by authors like Swiderski and others: the use of the reference to define the point of tangency and the use of partial warps as taxonomically important and useful shape variables in cladistics. Authors like Rohlf *et al.* (1996) suggest that species in a data set should be aligned so that the (x, y) co-ordinates of the landmarks can be averaged to obtain a reference or tangent configuration (or GLS reference). This reference configuration defines the point of tangency between non-linear shape space and the approximating linear tangent space in which the linear multivariate statistical analyses are performed. One wants a reference that yields the best approximation of shape, therefore the GLS mean should be used (personal communication, Rohlf). If another reference is chosen, the tangent space is redefined and a possibility therefore exists that different results will be obtained. The mean ancestral shape of any morphological structure (as chosen by Swiderski (1993)) should therefore not be considered as the reference configuration when geometric morphometric analysis is performed. The use of partial warps in cladistics is less clear, according to Rohlf (personal communication) there is probably no reason to expect partial warps to be good cladistic characters, no matter what is used as reference.

Fink & Zelditch (1995) proposed a new method to infer phylogeny from ontogenetic transformations of continuous morphological data, and coded ontogenetic regressions of shape and size to obtain discrete characters which they used in a parsimony analyses. They used partial warp scores obtained from thin-plate spline analysis as shape variables. Zelditch *et al.* (1995) analysed the body form of the piranhas (teleost fishes) and thin-plate splines decomposed by its partial warps to yield shape characters that were, according to

the authors, suitable for cladistic analysis.

The use of discrete characterisation of regressions of partial warp scored was criticised by Adams & Rosenberg 1998), and Rohlf (1998) aired theoretical objections to the use of partial warp scores as biological homologous characters. Characters found by most morphometric methods are unsuitable (under most conditions) for cladistic analysis because the test of similarity is the most difficult test of homology.

Another problem Adams & Rosenberg (1998) identified with the approaches of Fink & Zelditch (1995), was the use of the outgroup specimen as reference configuration for the study group (Swiderski, 1993 also used the ancestral shape as an alternative reference configuration for the study group, as discussed in a previous paragraph). Fink & Zelditch (1995) stated that only if an outgroup specimen is used for the starting form, shape deformations can be interpreted as actual evolutionary events. The average of juvenile specimens was used as reference form and the character states of the reference outgroup species were used to code characters of the other species in the data set. Specimens in the study group should, however, be aligned and the point of tangency between non-linear shape space and the approximating linear tangent space defined. This point of tangency is called the reference configuration or tangent configuration (Rohlf *et al.* 1996). Choosing another reference configuration (e.g. the ancestral shape or outgroup) would result in specifying another point of tangency, but only the mean will give the best fit of tangent space.

Adams & Rosenberg (1998) tested the protocol of Zelditch and co-workers by using a single species as reference outgroup. They also chose three alternative (arbitrary) bases for tangent space (found from three different rotations of the partial warp scores) and coded the ontogenetic shape regressions along the axes of the three new bases. The phylogeny of the study group was then re-estimated using the newly coded characters. Their conclusion was that the choice of the starting form (reference configuration) as well as the choice of a basis for tangent space has an impact on the resulting phylogeny. Different bases for tangent space result in a rigid rotation of partial warp scores. This, however, loses no information regarding the relationships among the taxa in tangent space. Adams & Rosenberg therefore concluded that the transformation of the rotated continuous data to discrete character states loses information about the relationship between the size and shape of taxa in a data set.

Other authors exploring the uses of geometric morphometrics include Loy *et al.* (1993). They analysed 13 landmarks recorded on the right half dorsal view of the skull of seven fossorial species in three genera of Old World Talpidae (Mammalia, Insectovora), by using centroid size to examine intra-specific and inter-specific variation. Shape differences among the species of the genus *Talpa* were also investigated using uniform and non-uniform shape components of the landmark data. Rohlf *et al.* (1996) took the landmark data produced by Loy *et al.* (1993) which consisted of 113 individuals of the three genera *Morgera*, *Talpa* and *Parascalops* and re-analysed it by using partial-warp scores as variables (to capture shape variation, rather than conventional linear measurements) in different multivariate statistical analyses such as principal component analysis, multivariate analysis of variance and canonical variate analysis. The aim of the study was to show how these standard methods can be used to test for shape differences among populations. One of the advantages in using these partial warp scores as variables is that trends in shape variation can be visualised as a continuous non-linear deformation.

Using geometric morphometrics in the analysis of the metendosternites

The ultimate question can now be asked: how can geometric morphometrics and phylogenetics be linked and used successfully to determine relationships between organisms? In the previous paragraphs, the term homology has been used to describe the landmarks identified and analysed in geometric morphometrics. A distinction must, however, be made between the "type" or definition of homology used by morphometric and phylogenetic techniques. Operational homology (or similarity relation defined by positional correspondences among landmarks) is traditionally associated with morphometrics and phenetics, while taxic homology (or corroborated synapomorphies e.g. shared, derived character states that are found in monophyletic groups) is traditionally associated with cladistics (Smith, 1990). Morphometrics may contribute to phylogenetics by quantifying comparative information about states in transformation series of homologous structures. These steps may provide characters for cladistic analysis or describe evolutionary trends in phylogenetic analysis (Smith, 1990).

Operational and taxic homology are often discussed as concepts that exclude each other's

validity (Smith, 1990). Each type or definition of homology, however, refers to a step in the process by which homologous characters are chosen and analysed in the study of evolution. Cladistics and morphometrics can be used together to estimate the sequence of lineage branching and the patterns of response among characters. Together, the cladistic tree and the morphometrically derived characters can provide information about the relative timing, amounts and directions of evolution (Smith, 1990).

In a two-dimensional space, shape can be described as a closed curve while in a three-dimensional space, shape can be described as a surface (Reyment, 1991). If we study the shape of the metendosternites of members of the Scarabaeoidea, it is clear that it forms corners, bulges and intersections around the outline of the structure. These features correspond to what we can describe as special points or characters associated with the specific form of these structures. In geometric morphometrics the term landmark is used for a specific homologous point along a biological structure (as discussed previously). In phylogenetic terms these points are called characters (and differences within a specific character, character states). Using geometric morphometric techniques to analyse the different landmarks is much more accurate than describing and comparing relative variation in the states of a character of the metendosternite of different groups.

Geometric morphometrics can be defined as the philosophy of shape-variability (Watson, 1989). The results from a geometric morphometrics analysis, therefore, describe the shape variations between different homologous landmarks on the metendosternites of the species belonging to the Scarabaeoidea.

Material and methods

OBTAINING DRAWINGS OF THE METENDOSTERNITES

Because the metendosternite is a rigid structure it lends itself to the analysis by geometric morphometric methods (landmark positions would therefore not change because of distortion of the material during handling). This structure varies between the different groups within the Scarabaeoidea, but within the groups, little difference is present (see Table 10.1 for a list of specimens). Only twelve of the thirteen families were compared with each other in the present study. Members of the Passalidae were excluded because of their unique metendosternite structure that made it impossible to compare with that of the other families.

Homologous landmarks between them could not be established beyond any doubt, and rather than choosing landmarks that might not be homologous, it was decided to exclude the family from the study (these reasons are discussed in detail in the discussion). (Drawings of the metendosternite of some species belonging to the Passalidae are shown in Appendix 10.1, at the end of this chapter).

Metendosternites were dissected from dried as well as alcohol preserved specimens. For clear visualisation, the metendosternites were first cleaned of muscle attachments. Various methods were experimented on, including boiling in water or KOH, with the best results obtained by soaking in a household bleach (e.g. JIK) for a few minutes depending on the amount of muscle attached. To avoid dissolving the chitin ofthe metendosternite, care was taken not to soak the material for too long. The cleaned metendosternites were then rinsed in water, air dried and stored in a dust free environment.

Attempts to draw the morphological structure of the metendosternites for geometric morphometrics proved to be very difficult, because of the critical need for an exact and consistent orientation of all the structures to be compared. To overcome this problem, each metendosternite was inverted on a microscope slide, with the ventral rib pointing at a 90° angle away from the microscope slide. The tips of the ventral transverse flanges, as well as the posterior end of the stalk, were glued onto the microscope slide using colourless glue that allowed dorsal lateral and ventral views to be drawn.

The lateral view was drawn by placing a slide in a block designed to orientate the slide at 90°. The frontal view was drawn by placing a slide in the same block, but with the frontal part facing upwards. The dorsal view was drawn by "hanging" an inverted slide between two blocks.

The drawings were then scanned using a flatbed scanner and images copied into a computer program called Adobe Photoshop LE which facilitated exportation to the tps series of programs (discussed in the following paragraphs) to perform the various geometric morphometric analyses. (Versions of the individual tps programs used, are mentioned later in the methods section). Phenograms were drawn with NTSYS-pc ((Rohlf, 1990 (Version 1.60) and 1993a (Version 1.80)).

As mentioned previously, the tps series of programs were employed to facilitate statistical analysis of landmark data in this thesis. Each individual program within the series performs a small task that will be discussed in the following paragraphs. Tps was found to be best suited for the analysis on the metendosternite landmark data, because it is not necessary for the biologist to manually work through the complicated mathematical steps to analyse the landmarks, and it presents a powerful tool to visualise shape changes in tangent space.

LANDMARK POSITIONS

To implement geometric morphometrics, different landmarks on the metendosternites are chosen. It is presumed that e.g. landmark no. 1 is homologous in all the organisms in the study group. The points or landmarks that are chosen for the study will determine the shape of the metendosternite. The shape of the metendosternite of each of the specimens will thus be represented by the "outline with landmarks".

The main advantage of geometric morphometrics is that it permits the description of variability of a biological structure amongst groups of organisms. The differences in shape between the two organisms are then shown as deviations.

tpsdig (James Rohlf, Version 1.08)

The purpose of this program is to facilitate the statistical analysis of landmark data in morphometrics by making it easier to collect and maintain landmark data from digitised images. The program is used to mark the location of the landmarks. It also allows one to capture outlines of structures. This procedure allows the digitisation of each landmark and its conversion into *x,y* co-ordinates that can be subjected to a series of statistical analyses available in tps.

Nine points on each of the frontal, 11 on the dorsal and 19 on the lateral views of the metendosternites for all taxa (families, or in the case of Scarabaeidae, each subfamily) considered were chosen. All points were consistent and easily identifiable between taxa.

DETERMINING WHETHER AMOUNT OF VARIATION IS SMALL ENOUGH FOR STATISTICAL ANALYSIS

Before the data sets for the three views (each containing the *x,y* co-ordinates of the consensus configuration for each family) of the metendosternites were analysed further, it was necessary to determine whether the observed variation in shape is sufficiently small that the distribution of points in the tangent space can be used as a good approximation of their distribution in shape space. The tpsSmall program (James Rohlf, Version 1.12) was used to determine whether the amount of variation in shape in each data set is small enough to permit statistical analyses to be performed in the tangent space (which is linear) approximate to Kendall's shape space (which is non-linear). In other words, tpsSmall helps one to assess the accuracy of the approximation of shape space by the tangent space. The least-squares regression slope (through the origin) and the correlation (uncentered) between the Procrustes distances and the Euclidean distance between all pairs were computed to measure their deviation from a linear relationship. TpsSmall can plot the distances in the tangent space versus Procrustes distances and if the scatter is close to a straight line, it implies that the approximation is good enough for the data set.

DETERMINING THE CONSENSUS CONFIGURATION FOR EACH TAXON

Because shape differences between families were studied, the average or consensus configuration of landmarks for each family was computed using tpsSuper (James Rohlf, Version 1.03) (for each of the three views). Orthogonal least-squares Procrustes average configuration of landmarks was computerised using generalised orthogonal least-squares procedures. A consistent alignment of species is needed, because the consensus configuration is the mean landmark configuration of the group of species for each family.

UNWARPING IMAGES OF EACH SPECIMEN WITHIN A TAXON

After determining the consensus configurations, the images of each specimen in each taxon was "unwarped" so that the landmarks coincide with their positions in the consensus configuration. The tpsSuper program (James Rohlf, Version 1.03) performs a least-squares orthogonal generalised Procrustes analysis, unwarps (using the thin-plate spline) the images for each specimen to the consensus configuration, and then averages the unwarped images. The fuzzy or out of focus areas in the mean or average image correspond to areas that vary

among specimens, whereas darker areas correspond to landmark positions of the consensus configuration.

CONSTRUCTING A REFERENCE (OR TANGENT) CONFIGURATION FOR EACH DATA SET AND THE ANALYSIS OF THE LANDMARK POSITIONS OF CONSENSUS CONFIGURATIONS OF THE DIFFERENT TAXA

The consensus configurations for each of the families were aligned so that the (*x,y*) co-ordinates of the landmarks can be averaged to obtain a reference configuration or tangent configuration (this was done for all three views of the metendosternites). Any data set can only possess one reference or tangent configuration. This tangent configuration of landmarks corresponds to the point of tangency between the exact non-linear shape space and the approximating tangent space in which linear multivariate statistical analysis can be performed (Rohlf *et al.*,1996). It can also be described as the average landmark configuration for a specific data set. The reference configuration was computed by tpsSplin (James Rohlf, Version 1.14), using the generalised least-squares Procrustes superimposition method or GLS (Gower, 1975; Rohlf & Slice, 1990).

CONSTRUCTION OF PHENETIC TREES AND DETERMINING PHENETIC RELATIONSHIPS BETWEEN THE FAMILIES

Procrustes distances (the square root of the sum of squared differences between corresponding points) between each of the families were computed, and a matrix from each of the views, obtained (the matrix was produced by the tpsSplin program (James Rohlf, Version 1.14)). The landmarks of the reference or tangent configuration (GLS) were strictly used to identify the tangent point in Euclidean space. Each of the triangular Procrustes distance matrices of the three views were subjected to UPGMA cluster analyses (unweighted pair group method using arithmetic averages) and phenetic trees (Sneath & Sokal, 1973) generated by NTSYS-pc (Rohlf, 1990; 1993a) to determine the phenetic relationships between taxa. One of the important advantages of using Procrustes distances to capture shape variation, is that these distances are considered the most reliable method to determine phenetic relationships between taxa (Goodall & Bose, 1987; Chapman, 1990; Rolph, 1990; Goodall, 1991; Marcus *et al.*, 1993). The reason why the Procrustes distance matrices of the three views is used to compute the phenetic trees is that these values are in

shape space and they are the only ones available to us that represent the actual distances between taxa, all other values are approximations of these distances.

ANALYSIS OF THE VARIATION BETWEEN TAXA USING THE NONAFFINE SHAPE VARIATION (RELATIVE WARPS)

In order to relate trends in shape change, relative warp analyses (RWA) were performed. An RWA is a principal components analysis (PCA) of the covariance matrix of the partial warp scores and is performed by the program, where á=0 (Bookstein, 1991). In other words, relative warps with á=0 is just a PCA of shape, and the shape is expressed in terms of partial warps, but not dependent upon them (Rohlf, personal communication). An alternative is also to perform a PCA of the aligned specimens, this will result in an identical ordination. Rohlf (1993b) suggested that á=0 should be used in these types of analyses, because á=0 presents morphometric differences at all scales (when á is greater that 0, geometrically small-scale variation is given less weight than the large-scale variation, the result is that of reducing the weight given to regions having more landmarks relative to the weight given to regions having fewer and therefore more widely spaced landmarks (Rohlf, *et al.*, 1996)). Relative warps are computed, using tpsRelw (James Rohlf, Version 1.16), to summarise the variation among the specimens (with respect to their partial warp scores) in as few dimensions as possible. Each relative warp can be plotted as a deformation of the space of the reference configuration of landmarks. The deformation can be viewed as displacements in which the reference object is deformed as a thin-plate spline in the positive or negative direction along a selected relative warp. The relative warp analyses are based on the nonaffine components of shape variation, which, according to Rohlf *et al.* (1996) dominate the estimate of overall morphological relationships. The first two relative warps usually are indicative of most of the variation between taxa, and therefore their scatter plot presents the most visual information about variation between families. Shape changes implied by variation along the first two relative warp axes can be shown as deformations using thin-plate splines. Thin-plate splines of the variation between any of the taxa can be drawn and shape variations between taxa, because of positional movement of landmarks, visualised. Shape features that are shared by phenetically close taxa can therefore be described, and compared to the respective phenograms of the data sets.

Results

ILLUSTRATIONS OF THE METENDOSTERNITES

Drawings of the metendosternites of the superfamily are presented in figures 10.1 to 10. 63. Landmark positions are shown on the different metendosternite views of the *Glaresis* sp. (Glaresidae). A list of studied species in each taxon is provided in Table 10.1. Note that scale is not important, because this is an analyses of shape.

Table10.1 List of code numbers, families and species of Scarabaeoidea used in this study.

Family number	**Family**	**Species names (and subfamilies for Scarabaeidae)**
1	Glaresidae	*Glaresis* sp.
2	Lucanidae	*Prosopocoilus natalensis*, *Macrodorcus rectus*, *Platyceropsis* sp., *Nippodorcus rubrofemoratus*, *Syndesus cornutus*, *Sinodendron rugosum*, *Ceruchus* sp.
3	Diphyllostomatidae	*Diphyllostoma* sp.
4	Glaphyridae	*Lichnanthe rathvoni*
5	Trogidae	*Omorgus melancholicus*, *Omorgus suberosus*, *Omorgus squalidus*, *Trox consimilis*, *Polynoncus pedestris*
6	Bolboceratidae	*Prototrupes copridoides*, *Eucanthus lazarus*, *Pseudathyreus orientalis*, *Athyreus bifurcatus*, *Neoathyreus panamensis*
7	Pleocomidae	*Pleocoma shostensis*, *Pleocoma simbriata*, *Pleocoma richseckeri*, *Pleocoma* sp.
8	Geotrupidae	*Frickius variolosus*, *Taurocerastes* sp., *Geotrupes spiniger*, *Thorectus cheisinus*, *Lethrus carinatus*
9	Ochodaeidae	*Ochodaeus kansasus*, *Ochodaeus repondus*, *Synochodaeus cucullus*
10	Ceratocanthidae	Ceratocanthidae sp.
11	Hybosoridae	*Phaeochrous mashunus*, *Hybosorus illegri*, *Liparochrus fossulatus*, *Coelodus cataneus*

12	Scarabaeidae	Aphodiinae: *Aphodius russatus*, *Aphodius septemmaculatus*, *Aphodius porcus*, *Colobopterus maculicollis*, *Pseudaphodius rufiventris*, *Ataenius alternatus* Scarabaeinae: *Onthophagus ferrox*, *Sisyphus* sp., *Kheper* sp., *Circellium bacchus*, Coprini sp., *Cephalodesmius armiger* Orphninae: *Orphnus capensis* Melolonthinae: *Isonychus pictus*, *Liparetrus* sp., Melolonthinae sp. 2, Melolonthinae sp. 3, Melolonthinae sp. 6, Melolonthinae sp. 7 Rutelinae: *Anomala daimaina*, *Anomala testaceipennis*, *Callcodes frenchi*, *Stigoderma sulcipennis*, Rutelinae sp. 1, Rutelinae sp. 2 Hopliinae: Hopliinae sp. 1, 2 and 3 Dynastinae: *Heteronychus arator*, *Dyscinetus dubius*, *Aspidolea* sp., Dynastinae sp. 1 Trichiinae: *Gnorimella* sp. Cetoniinae: *Cetonia roelofsi*, *Porphyronota maculatissima*, *Hypselogenia geotrupina*, *Diplognatha silicea* Valginae: Valginae sp.

FRONTAL VIEWS OF METENDOSTERNITES

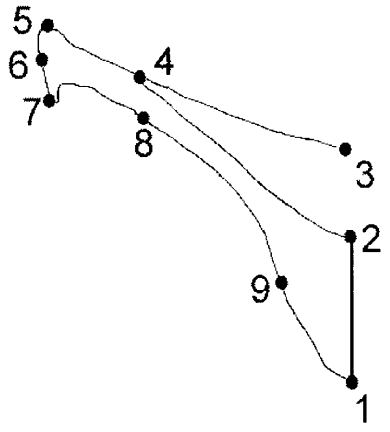


Fig. 10. 1 A

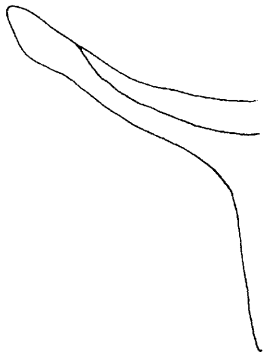


Fig 10.2 A

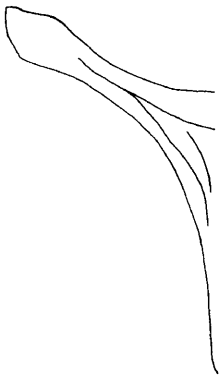


Fig. 10.2 B

Fig. 10.1 Frontal view of metendosternite: A, *Glaresis* sp. (Glaresidae), with landmark positions

Fig. 10.2 Frontal view of metendosternite: A, *Prosopocoilus natalensis* and B, *Macrodorcus rectus* (Lucanidae)

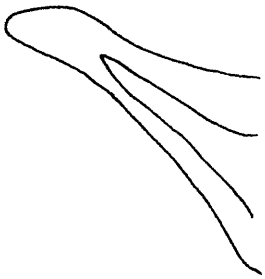


Fig. 10.2 C

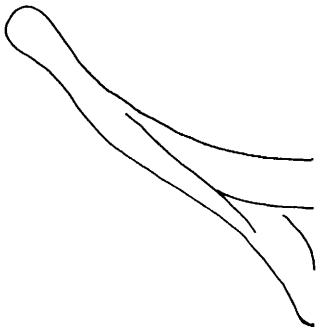


Fig. 10.2 D

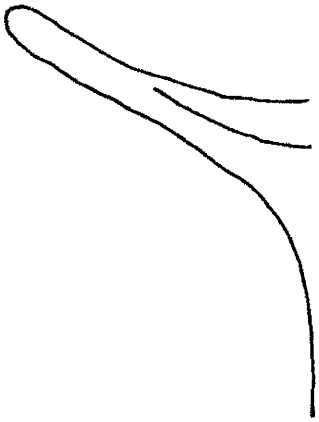


Fig.10.2 E

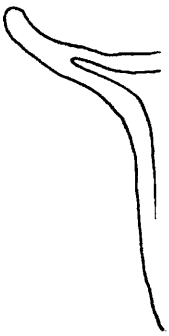


Fig 10.2 F

Fig. 10.2 G

Fig 10.2 Frontal view of metendosternite: C, *Platyceropsis* sp.; D, *Nippodorcus rubrofemoratus*; E, *Syndesus cornutus*; F, *Sinodendron rugosum* and G, *Ceruchus* sp. (Lucanidae)

Fig. 10.3 A

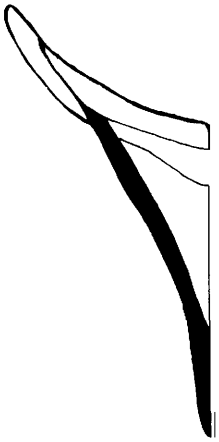


Fig. 10.4 A

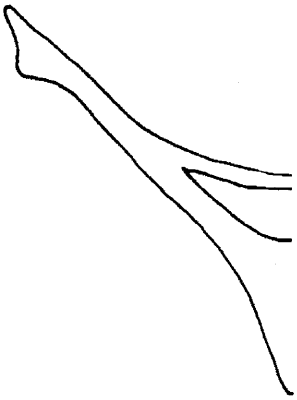


Fig. 10.5 A

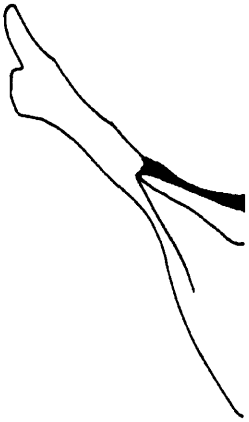


Fig. 10.5 B

Fig. 10.3 Frontal view of metendosternite: A, *Diphyllostoma* sp. (Diphyllostomatidae)

Fig. 10.4 Frontal view of metendosternite: A, *Lichnanthe rathvoni* (Glaphyridae)

Fig. 10.5 Frontal view of metendosternite: A, *Omorgus melancholicus* and B, *Omorgus suberosus* (Trogidae)

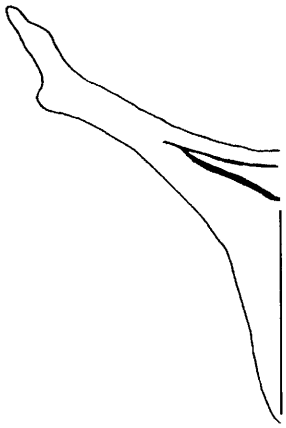


Fig. 10.5 C

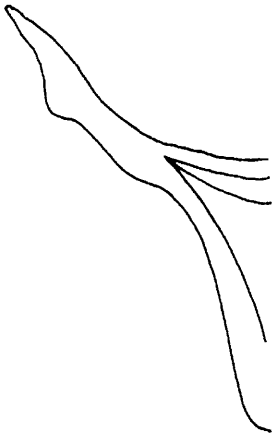


Fig. 10.5 D

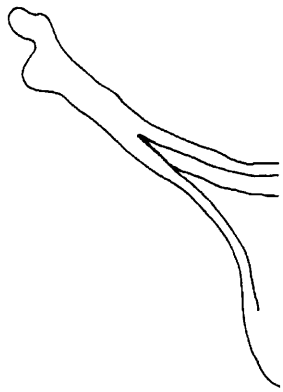


Fig. 10.5 E

Fig. 10.5 Frontal view of the metendosternite: C, *Omorgus squalidus* D, *Trox consimilis* and E, *Polynoncus pedestris* (Trogidae)

Fig. 10.6 A

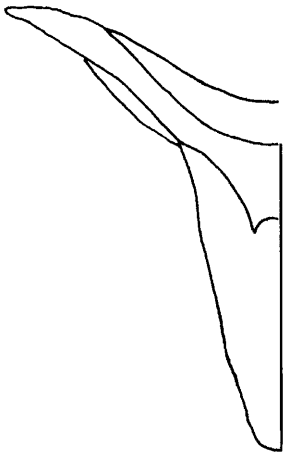


Fig. 10.6 B

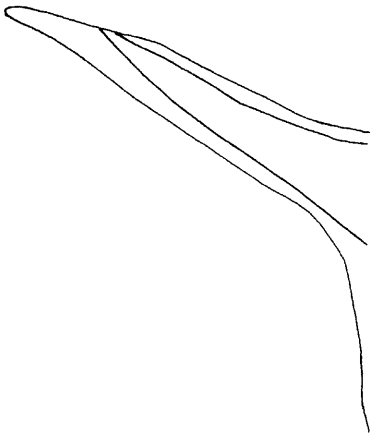


Fig. 10.6 C

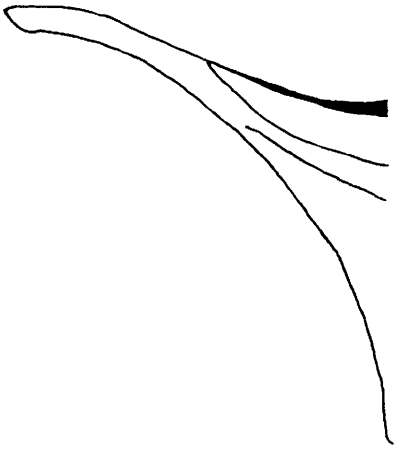


Fig. 10.6 D

Fig. 10.6 Frontal view of Metendosternite: A, *Prototrupes copridoides*; B, *Eucanthus lazarus;* C, *Pseudathyreus orientalis* and D, *Athyreus bifurcatus* (Bolboceratidae)

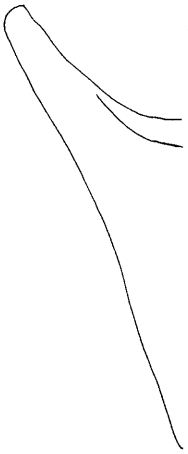


Fig. 10.6 E

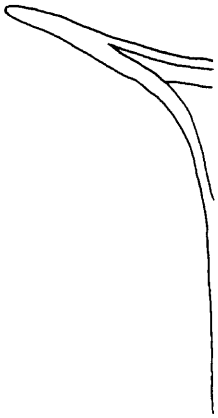


Fig. 10.7 A

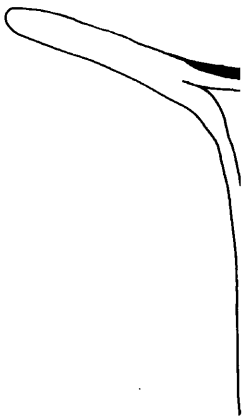


Fig. 10.7 B

Fig. 10.6 Frontal view of the metendosternite: E, *Neoathyreus panamensis* (Bolboceratidae)

Fig. 10.7 Frontal view of the metendosternite: A, *Pleocoma shostensis* and B, *Pleocoma simbriata* (Pleocomidae)

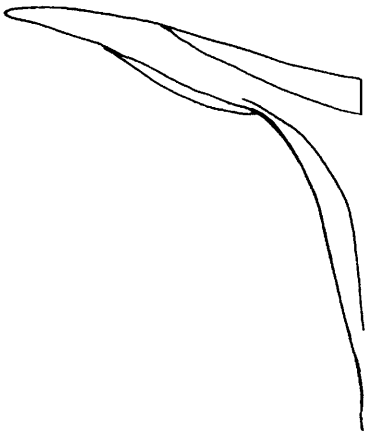


Fig. 10.7 C

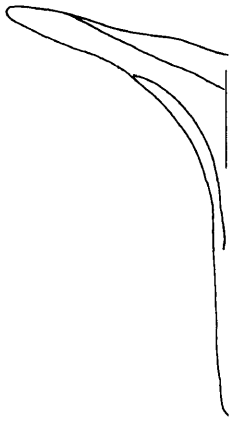


Fig. 10.7 D

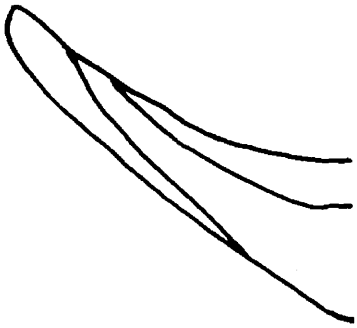


Fig. 10.8 A

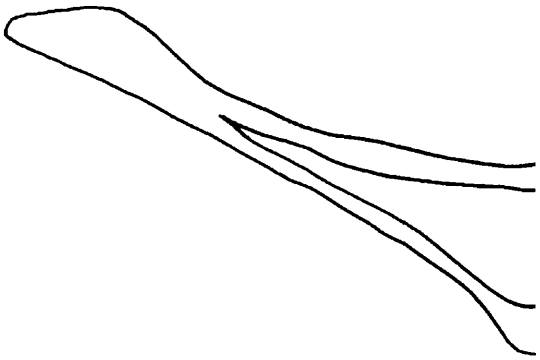


Fig. 10.8 B

Fig. 10. 7 Frontal view of the metendosternite: C *Pleocoma richseckeri* and D *Pleocoma* sp. (Pleocomidae)

Fig. 10.8 Frontal view of the metendosternite: A, *Frickius variolosus* and B, *Taurocerastes* sp. (Geotrupidae)

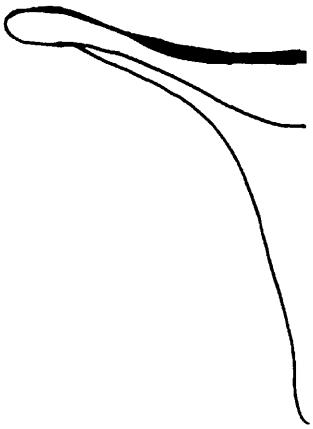


Fig. 10.8 C

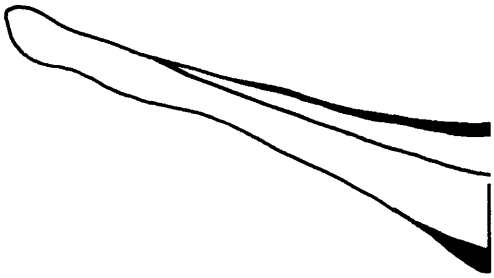


Fig. 10.8 D

Fig. 10.8 E

Fig. 10.8 Frontal view of the metendosternite: C, *Geotrupes spiniger*; D, *Thorectus cheisinus* and E, *Lethrus carinatus* (Geotrupidae)

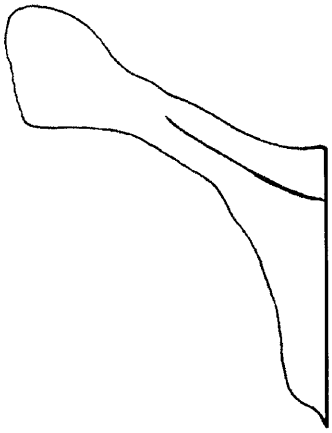


Fig. 10.9 A

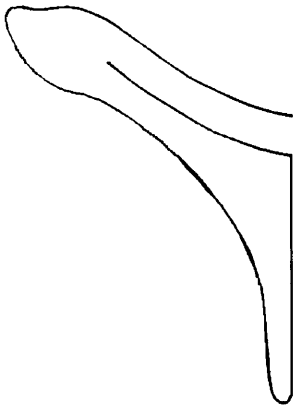


Fig. 10.9 B

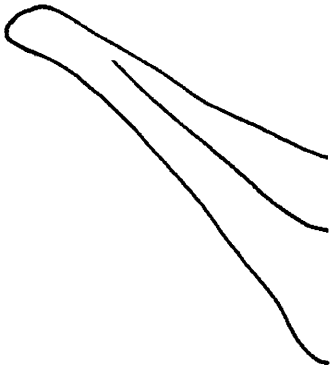


Fig. 10.9 C

Fig. 10.10

Fig. 10.9 Frontal view of metendosternite: A, *Ochodaeus kansasus*; B, *Ochodaeus repondus* and C, *Synochodaeus cucullus* (Ochodaeidae)

Fig. 10.10 Frontal view of metendosternite: A, Ceratocanthidae sp. (Ceratocanthidae)

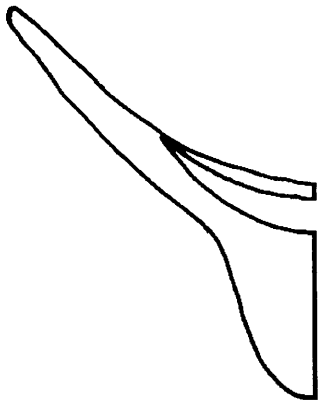


Fig. 10.11 A

Fig. 10.11 B

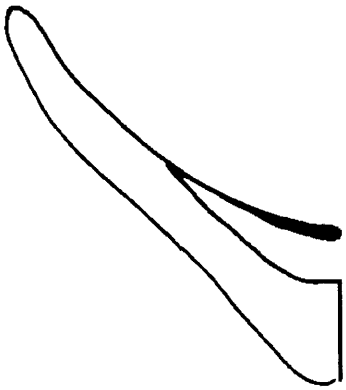


Fig. 10.11 C

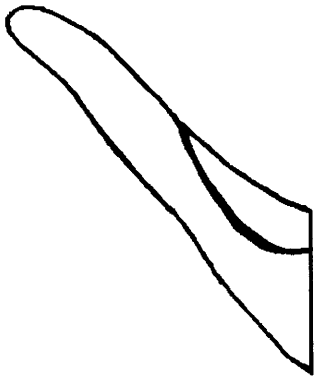


Fig. 10.11 D

Fig. 10.11 Frontal view of metendosternite: A, *Phaeochrous mashunus*; B, *Hybosorus illegri*, C, *Liparochrus fossulatus* and D, *Coelodus cataneus* (Hybosoridae)

Fig. 10.12 A

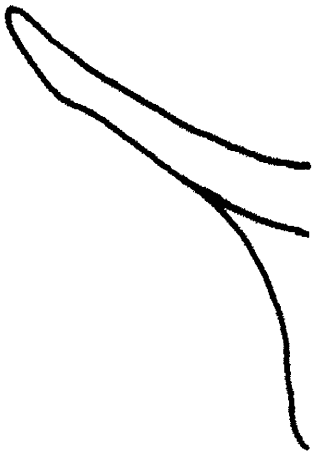


Fig. 10.12 B

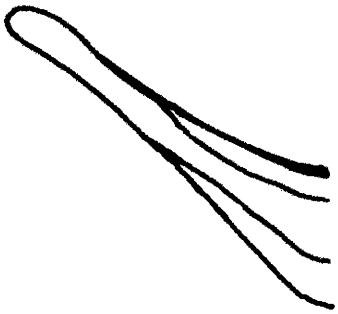


Fig. 10.12 C

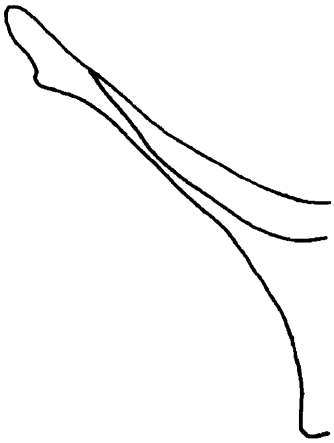


Fig. 10.12 D

Fig. 10.12 Frontal view of metendosternite: A, *Aphodius russatus*; B, *Aphodius septemmaculatus,* C, *Aphodius porcus* and D, *Colobopterus maculicollis* (Scarabaeidae: Aphodiinae)

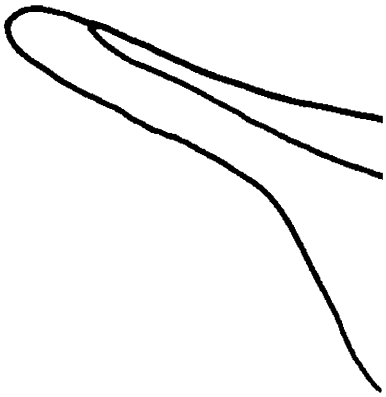


Fig. 10.12 E

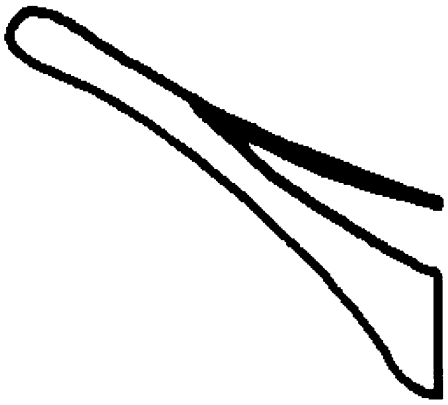


Fig. 10.12 F

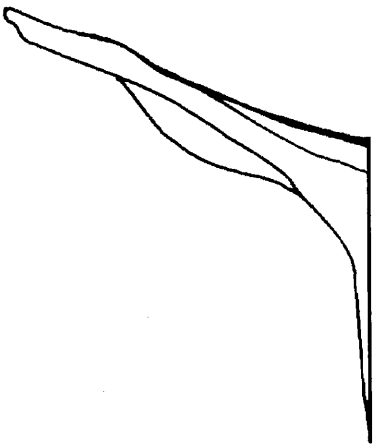


Fig. 10.13 A

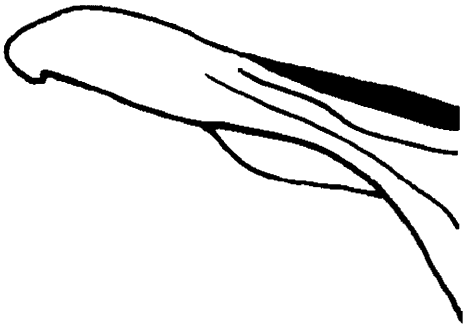


Fig. 10.13 B

Fig. 10.12 Frontal view of metendosternite: E, *Pseudaphodius rufiventris* and F, *Ataenius alternatus* (Scarabaeidae: Aphodiinae)

Fig. 10.13 Frontal view of metendosternite: A, *Onthophagus ferrox* and B, *Sisyphus* sp.(Scarabaeidae: Scarabaeinae)

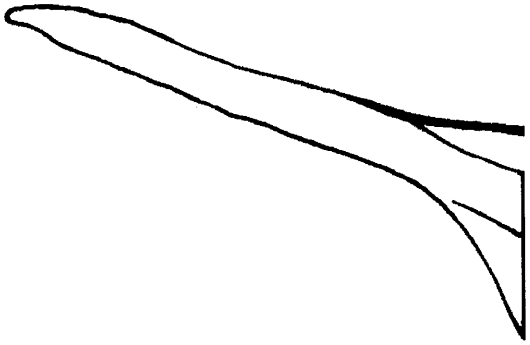


Fig. 10.13 C

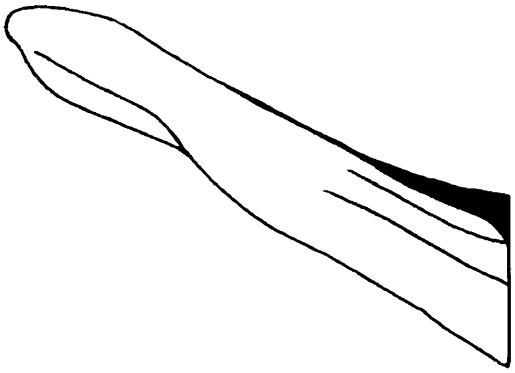


Fig. 10.13 D

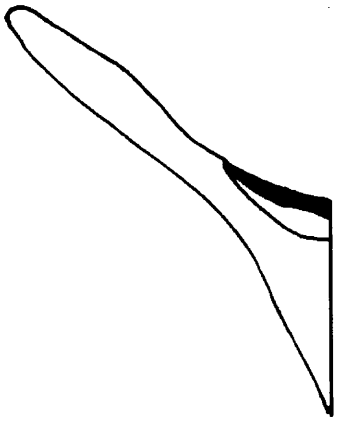


Fig. 10.13 E

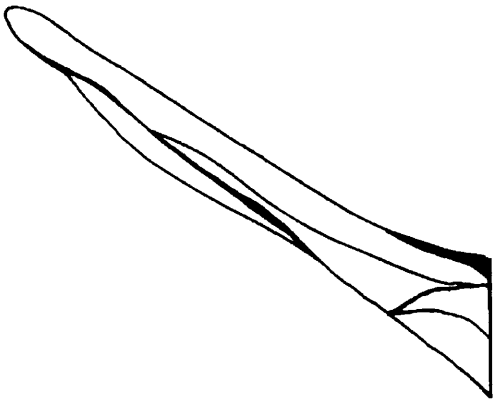


Fig. 10.13 F

Fig. 10.13 Frontal view of metendosternite: C, *Kheper* sp.; D, *Circellium bacchus*; E, Coprini sp. and F, *Cephalodesmius armiger* (Scarabaeidae, Scarabaeinae)

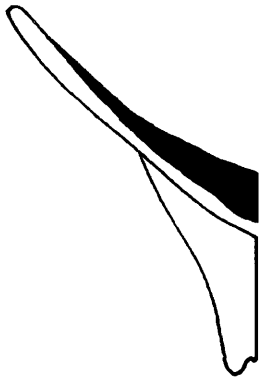


Fig. 10.14 A

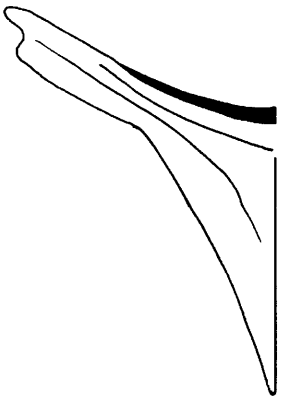


Fig. 10.15 A

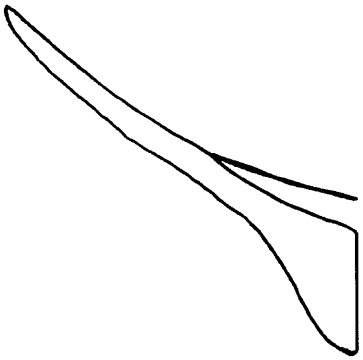


Fig. 10.15 B

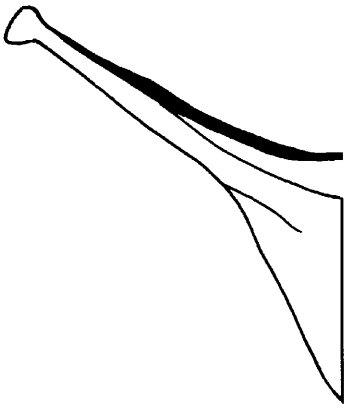


Fig. 10.15 C

Fig. 10.14 Frontal view of metendosternite: A, *Orphnus capensis* (Scarabaeidae: Orphninae)
Fig. 10.15 Frontal view of metendosternite: A, *Isonychus pictus* B, *Liparetrus lepidopygus* and C, *Diphucephala* sp. (Scarabaeidae: Melolonthinae)

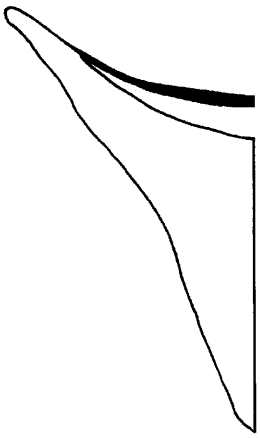


Fig. 10.15 D

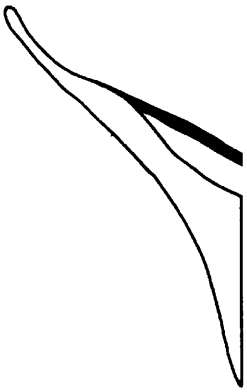


Fig. 10.15 E

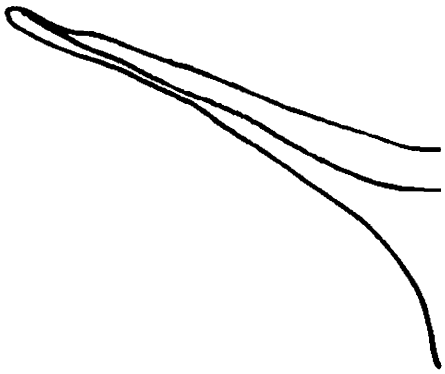


Fig. 10.15 F

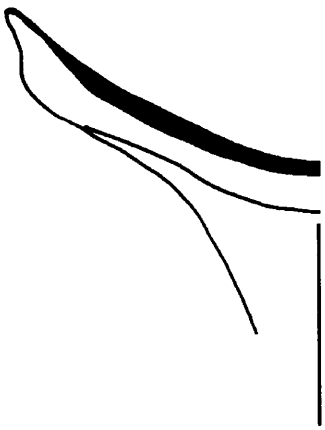


Fig. 10.15 G

Fig. 10.15 Frontal view of metendosternite: D, Melolonthinae sp 2; E, Melolonthinae sp. 3; F, Melolonthinae sp. 6; G, Melolonthinae sp. 7 (Scarabaeidae: Melolonthinae)

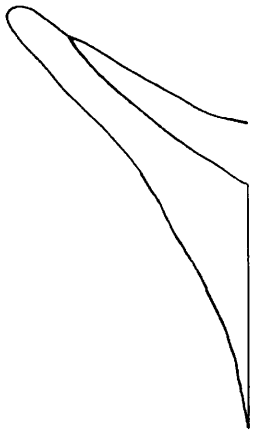


Fig. 10.16 A

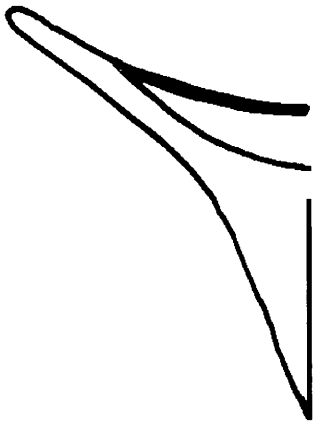


Fig. 10.16 B

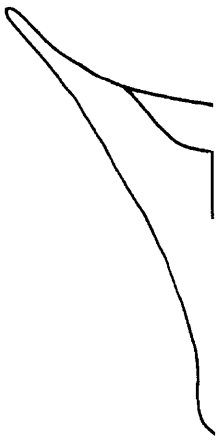


Fig. 10.16 C

Fig. 10.16 Frontal view of metendosternite: A, Hopliinae sp. 1; B, Hopliinae sp. 2 and C, Hopliinae sp. 3 (Scarabaeidae: Hopliinae)

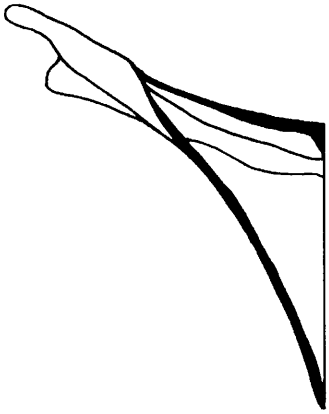


Fig. 10.17 A

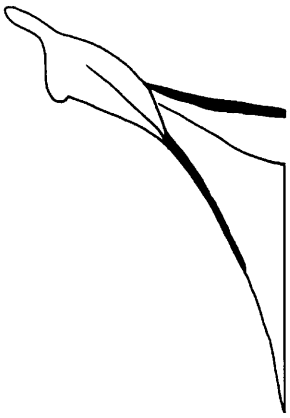


Fig. 10.17 B

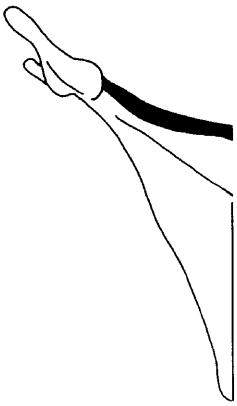


Fig. 10.17 C

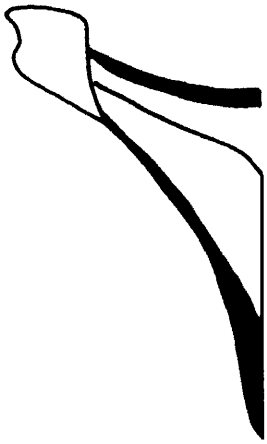


Fig. 10.17 D

Fig. 10.17 Frontal view of metendosternite: A, *Anomala daimaina*; B, *Anomala testaceipennis*; C, *Callcodes frenchi* and D, *Stigoderma sulcipennis* (Scarabaeidae: Rutelinae)

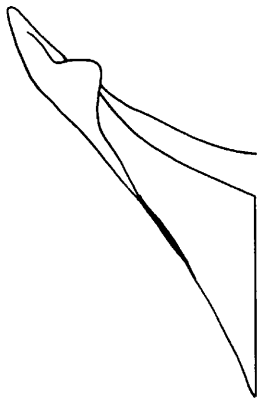


Fig. 10.17 E

Fig. 10.17 F

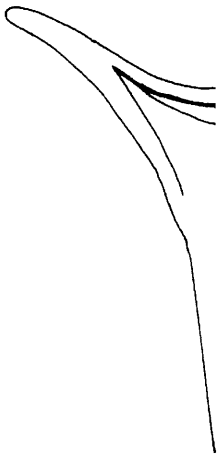


Fig. 10. 18 A

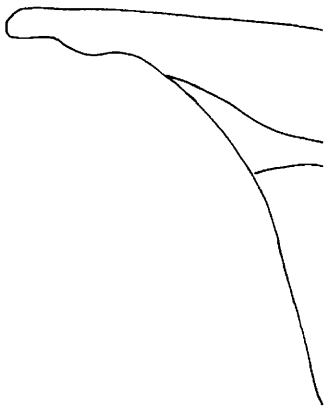


Fig. 10.18 B

Fig. 10.17 Frontal view of metendosternite: E, Rutelinae sp. 1; F, Rutelinae sp. 2 (Scarabaeidae: Rutelinae)

Fig. 10.18 Frontal view of metendosternite: A, *Heteronychus arator* and B, *Dyscinetus dubius* (Scarabaeidae: Dynastinae)

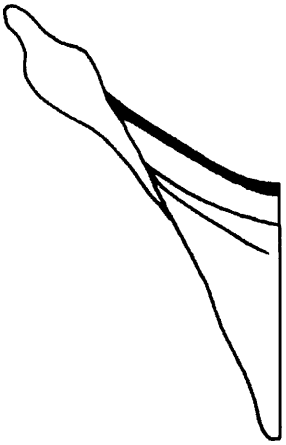


Fig. 10.18 C

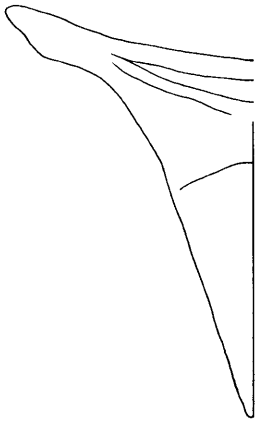


Fig. 10.18 D

Fig. 10.19 A

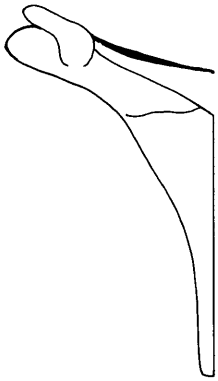


Fig. 10.20 A

Fig. 10. 18 Frontal view of metendosternite: C, *Aspidolea* sp. and D, Dynastinae sp. 1 (Scarabaeidae: Dynastinae)

Fig. 10.19 Frontal view of metendosternite: A, *Gnorimella* sp.(Scarabaeidae: Trichinae)

Fig. 10.20 Frontal view of metendosternite: A, *Cetonia roelofsi* (Scarabaeidae: Cetoniinae)

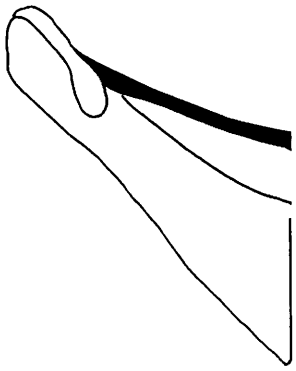


Fig. 10.20 B

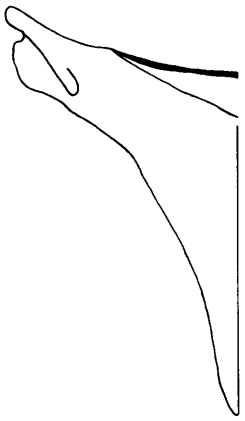


Fig. 10.20 C

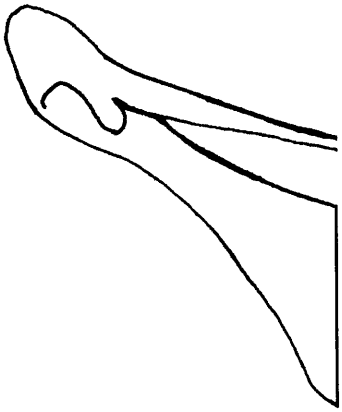


Fig. 10.20 D

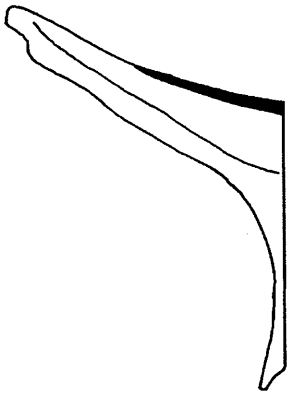


Fig. 10.21 A

Fig. 10.20 Frontal view of metendosternite: B, *Porphyronota maculatissima*; C, *Hypselogenia geotrupina* and D, *Diplognatha silicea* (Scarabaeidae: Cetoniinae)

Fig. 10.21 Frontal view of metendosternite: A, Valginae sp. (Scarabaeidae: Valginae)

DORSAL VIEWS OF METENDOSTERNITES

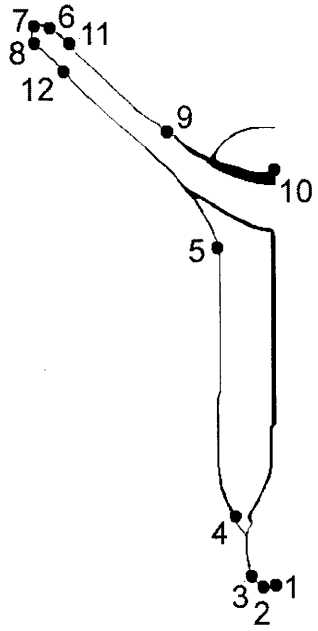


Fig. 10. 22 A

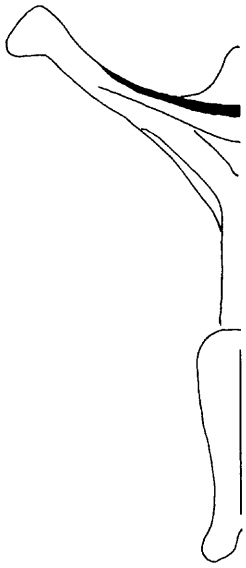


Fig.10.23 A

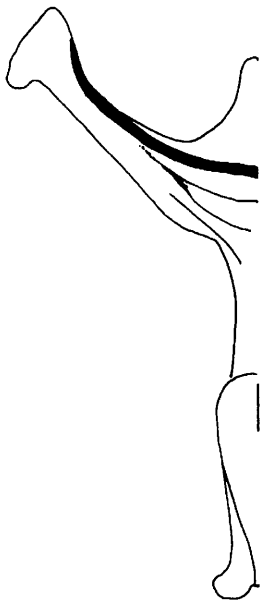


Fig. 10.23 B

Fig. 10.22 Dorsal view of metendosternite: A, *Glaresis* sp. (Glaresidae), with landmark positions

Fig. 10.23 Dorsal view of metendosternite: A, *Prosopocoilus natalensis* and B, *Macrodorcus rectus* (Lucanidae)

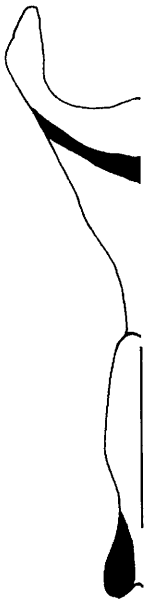


Fig. 10.23 C

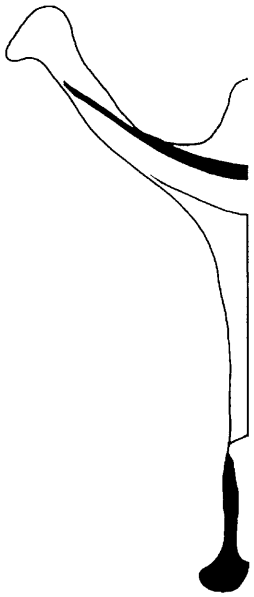


Fig. 10.23 D

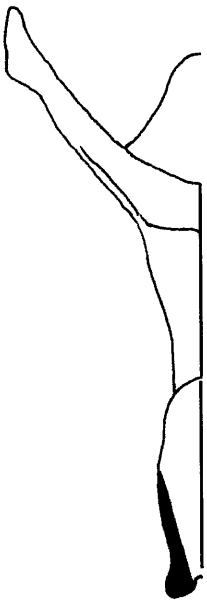


Fig. 10.23 E

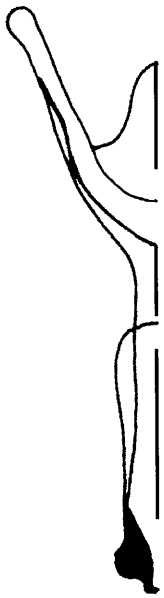


Fig. 10.23 F

Fig 10.23 Dorsal view of metendosternite: C, *Platyceropsis* sp.; D, *Nippodorcus rubrofemoratus;* E, *Syndesus cornutus* and F, *Ceruchus* sp. (Lucanidae)

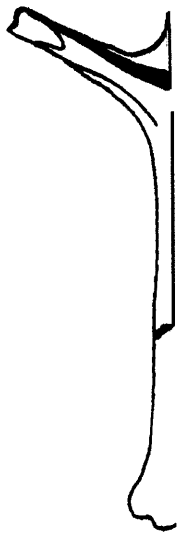


Fig. 10.24 A

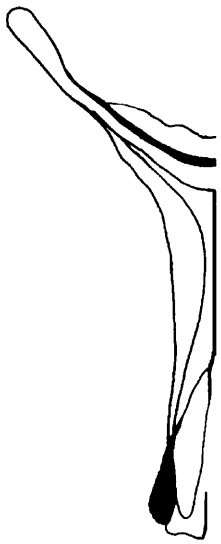


Fig. 10.25 A

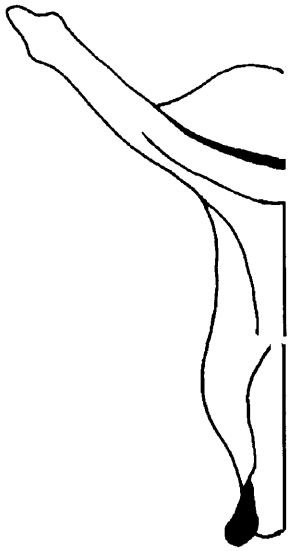


Fig. 10.26 A

Fig. 10.26 B

Fig. 10.24 Dorsal view of metendosternite: A, *Diphyllostoma* sp. (Diphyllostomatidae)

Fig. 10.25 Dorsal view of metendosternite: A, *Lichnanthe rathvoni* (Glaphyridae)

Fig. 10.26 Dorsal view of metendosternite: A, *Omorgus melancholicus* and B, *Omorgus suberosus* (Trogidae)

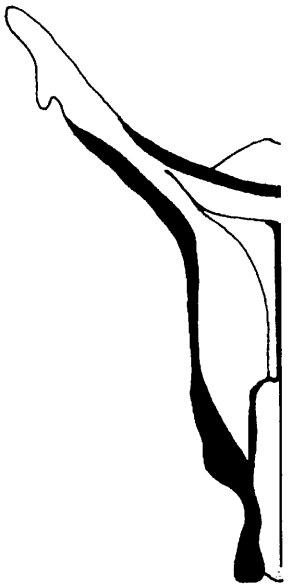


Fig. 10.26 C

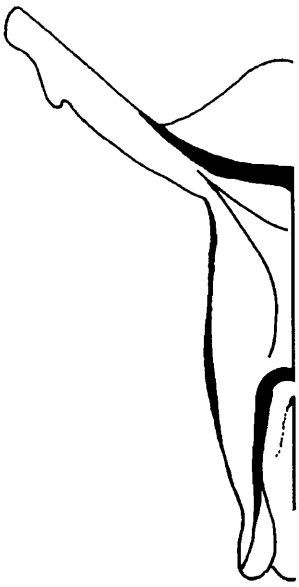


Fig. 10.26 D

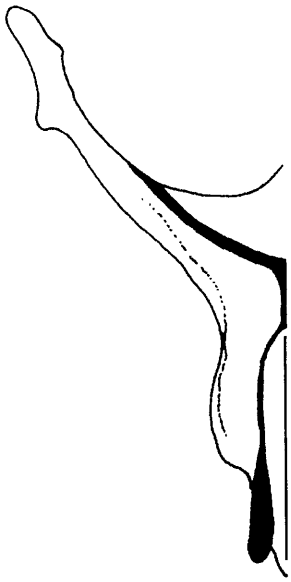


Fig. 10.26 E

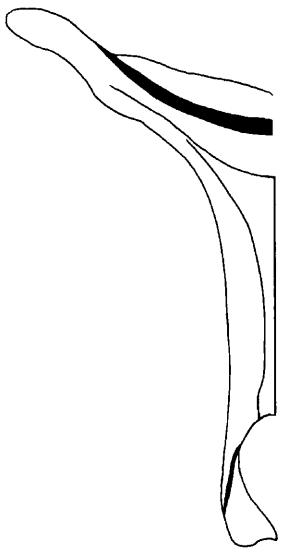


Fig. 10.27 A

Fig. 10.26 Frontal view of the metendosternite: C, *Omorgus squalidus,* D, *Trox consimilis* and E, *Polynoncus pedestris* (Trogidae)

Fig. 10.27 Dorsal view of metendosternite A, *Neoathyreus panamensis* (Bolboceratidae)

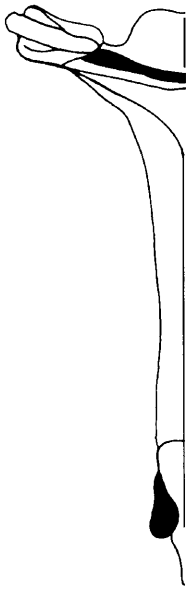


Fig. 10.27 B

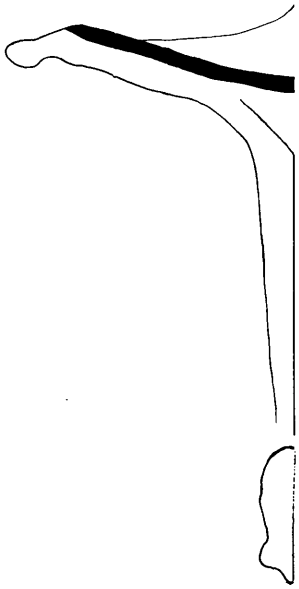


Fig. 10.27 C

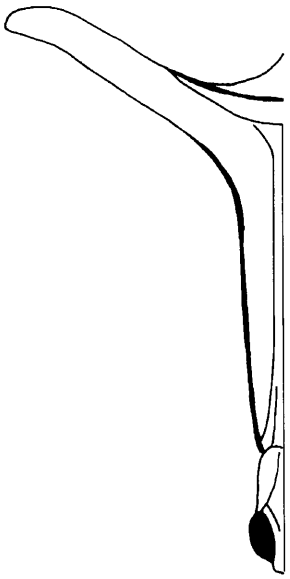


Fig. 10.27 D

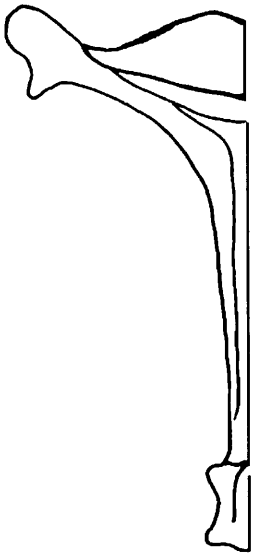


Fig. 10.27 E

Fig. 10.27 Frontal view of Metendosternite: B, *Eucanthus lazarus*; C, *Pseudathyreus orientalis*; D, *Athyreus bifurcatus* and E, *Prototrupes copridoides* (Bolboceratidae)

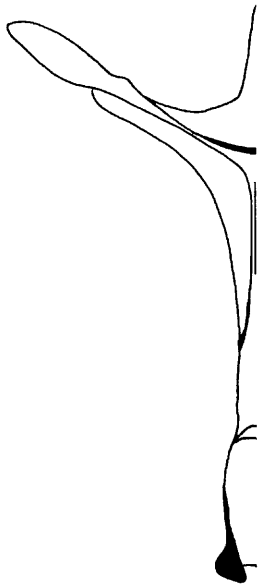


Fig. 10. 28 A

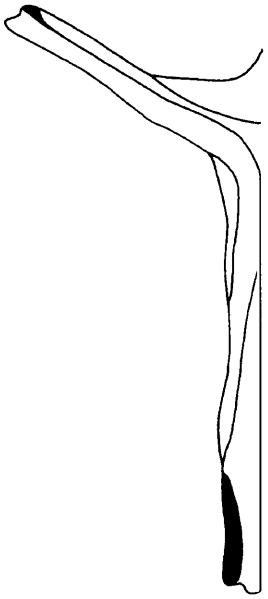


Fig. 10.28 B

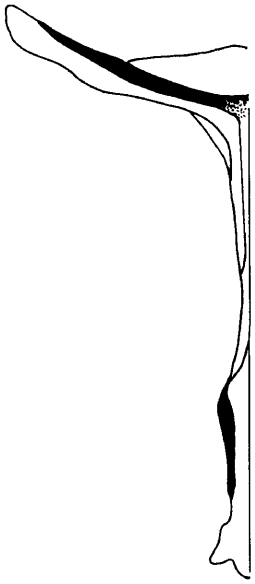


Fig. 10.28 C

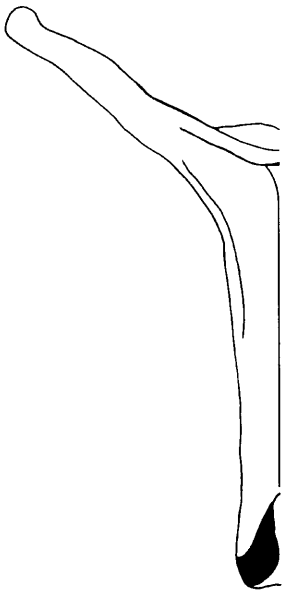


Fig. 10.29 A

Fig. 10.28 Dorsal view of the metendosternite: A, *Pleocoma shostensis* and B, *Pleocoma richseckeri* and C, *Pleocoma* sp. (Pleocomidae)

Fig. 10.29 Dorsal view of metendosternite: A, *Frickius variolosus* (Geotrupidae)

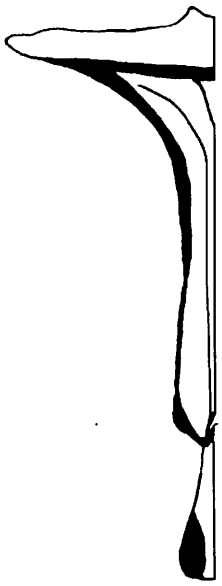


Fig. 10.29 B

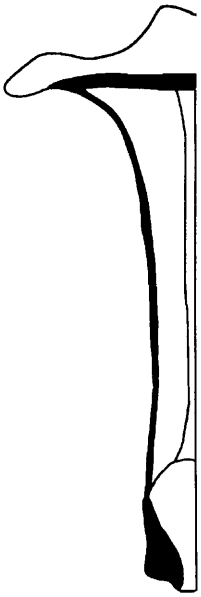


Fig. 10.29 C

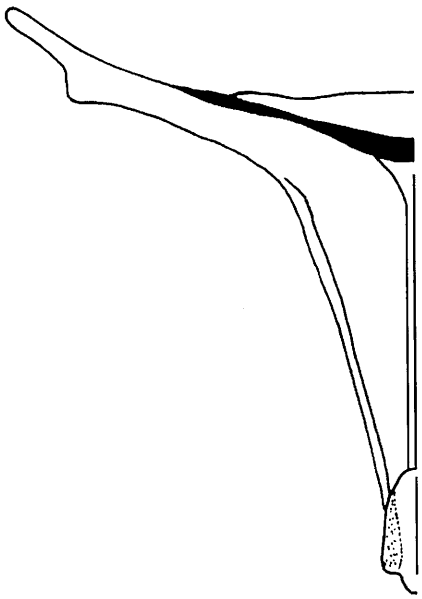


Fig. 10.29 D

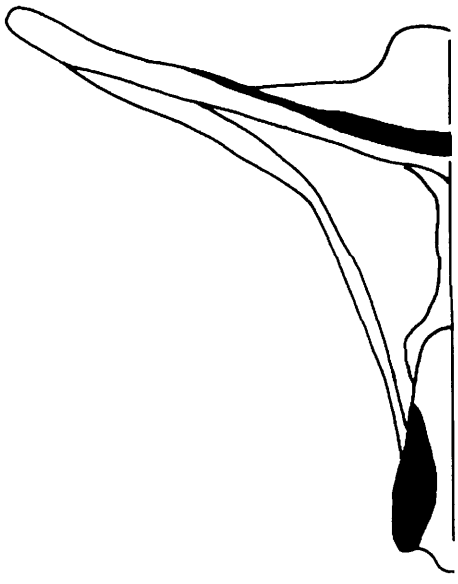


Fig.10.29 E

Fig. 10.29 Dorsal view of the metendosternite: B, *Taurocerastes* sp.; C, *Geotrupes spiniger*; D, *Thorectus cheisinus* and E, *Lethrus carinatus* (Geotrupidae)

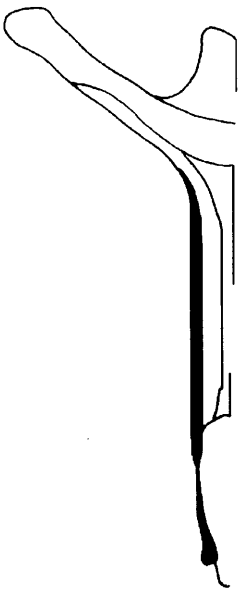


Fig. 10.30 A

Fig. 10.30 B

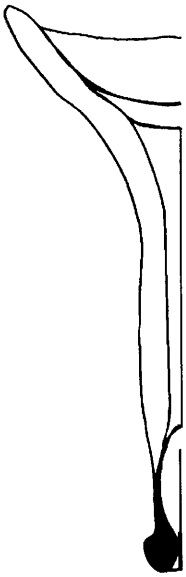


Fig. 10.30 C

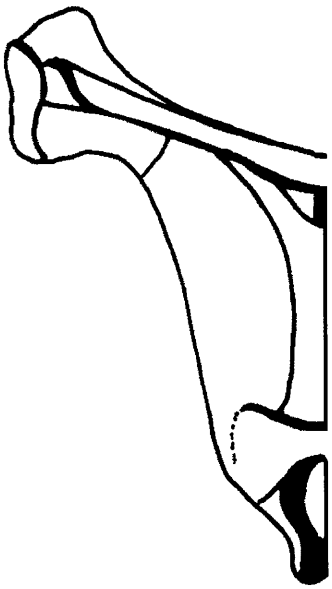


Fig. 10.31 A

Fig. 10.30 Dorsal view of metendosternite: A, *Ochodaeus kansasus*; B, *Ochodaeus repondus* and C, *Synochodaeus cucullus* (Ochodaeidae)

Fig.10.31 Dorsal view of metendosternite: A, Ceratocanthidae sp. (Ceratocanthidae)

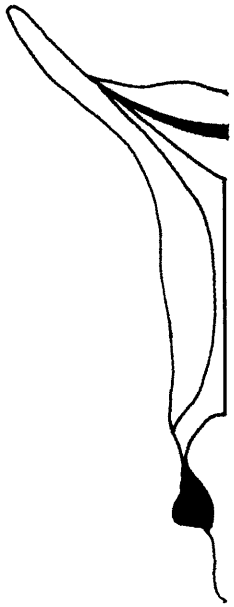


Fig. 10.32 A

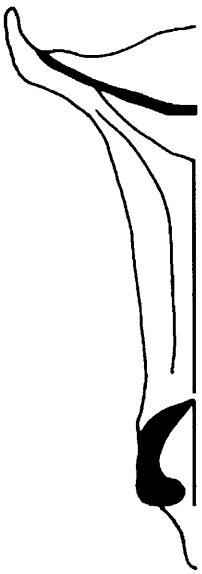


Fig. 10.32 B

Fig. 10.32 C

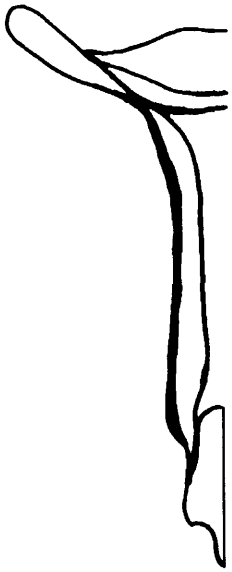


Fig. 10.32 D

Fig. 10.32 Dorsal view of metendosternite: A, *Phaeochrous mashunus*; B, *Hybosorus illegri*, C, *Liparochrus fossulatus* and D, *Coelodus cataneus* (Hybosoridae)

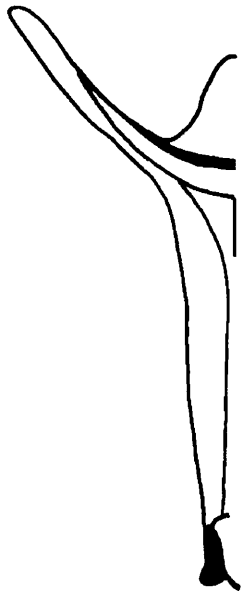


Fig. 10.33 A

Fig. 10.32 B

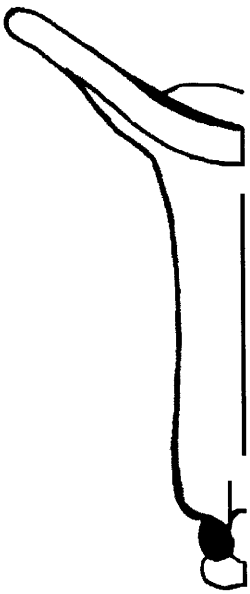


Fig. 10.33 C

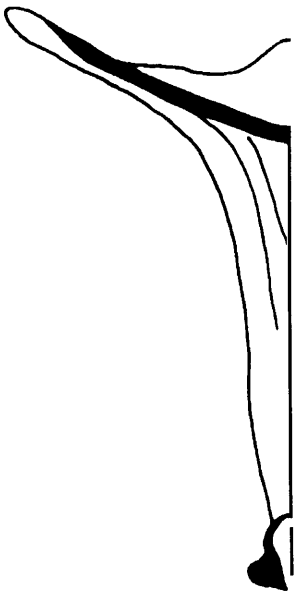


Fig. 10.33 D

Fig. 10.33 Dorsal view of metendosternite: A, *Aphodius russatus*; B, *Aphodius septemmaculatus,* C, *Aphodius porcus* and D, *Colobopterus maculecollis* (Scarabaeidae: Aphodiinae)

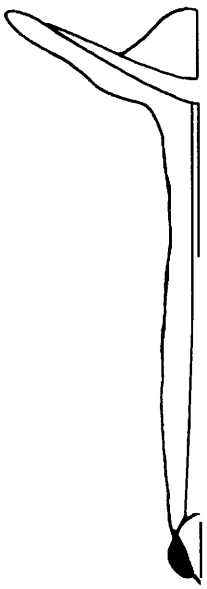


Fig. 10.33 E

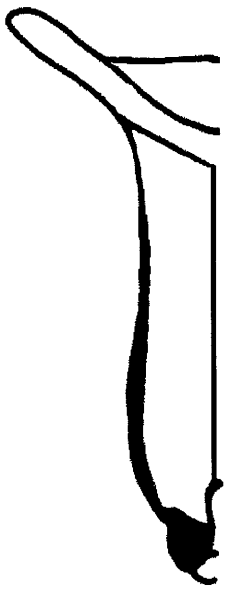


Fig. 10.33 F

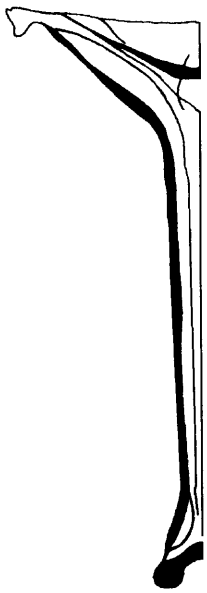


Fig. 10.34 A

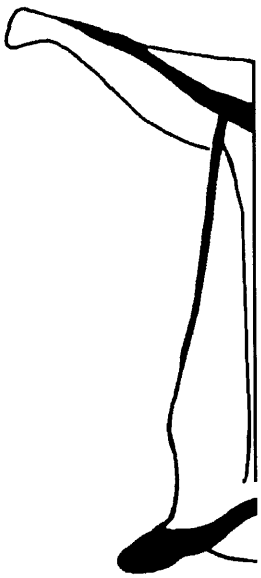


Fig. 10.34 B

Fig. 10.33 Dorsal view of metendosternite: E, *Pseudaphodius rufiventris* and F, *Ataenius alternatus* (Scarabaeidae: Aphodiinae)

Fig. 10.34 Dorsal view of metendosternite: A, *Onthophagus ferrox* and B, *Sisyphus* sp.(Scarabaeidae: Scarabaeinae)

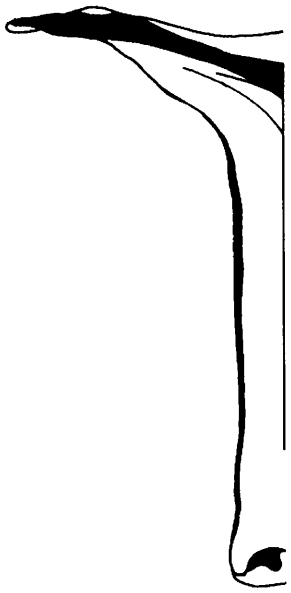


Fig. 10.34 C

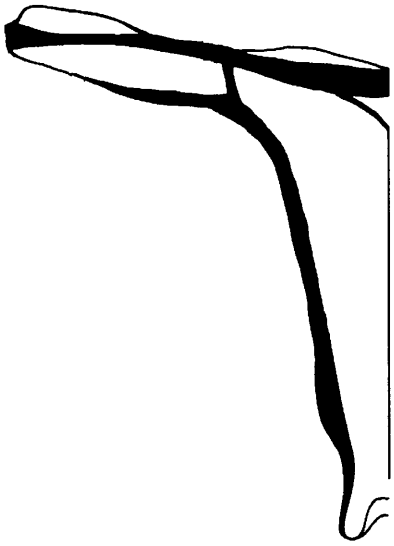


Fig. 10.34 D

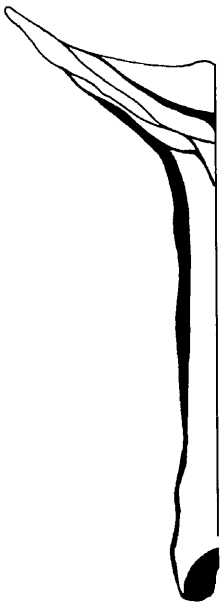


Fig. 10.34 E

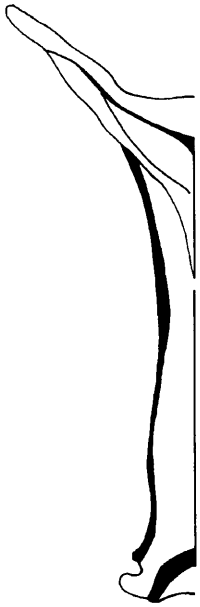


Fig. 10.34 F

Fig. 10.34 Dorsal view of metendosternite: C, *Kheper* sp.; D, *Circellium bacchus*; E, *Canthon* sp. and F, *Onitis caffer* (Scarabaeidae, Scarabaeinae)

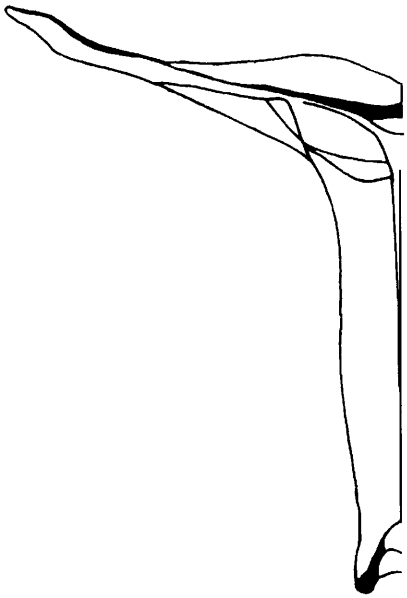


Fig. 10. 34 G

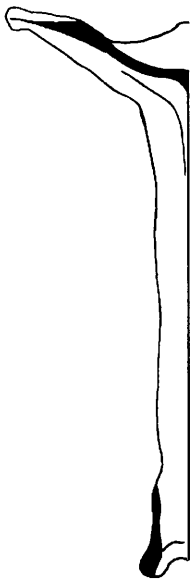


Fig. 10.34 H

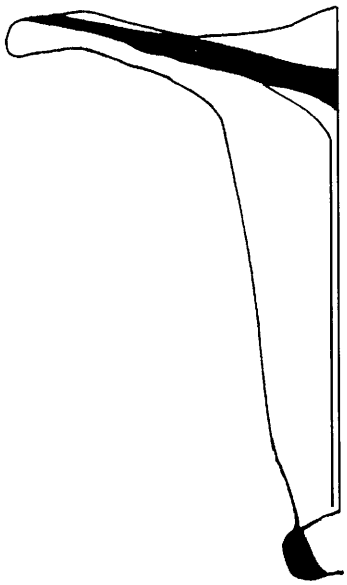


Fig. 10. 34 I

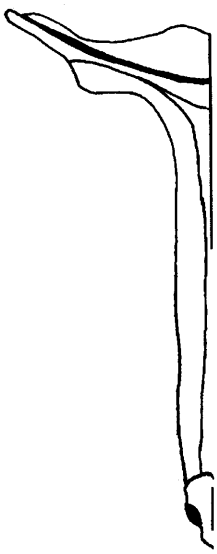


Fig. 10. 35 A

Fig. 10.34 Dorsal view of metendosternite: G, *Cephalodesmius armiger*; H, Coprini sp.; and I, Pinotini sp. (Scarabaeidae: Scarabaeinae)

Fig. 10.35 Dorsal view of metendosternite: A, *Orphnus capensis* (Scarabaeidae: Orphninae)

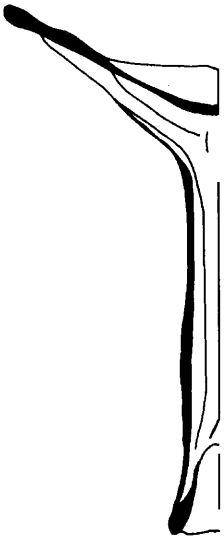


Fig. 10.36 A

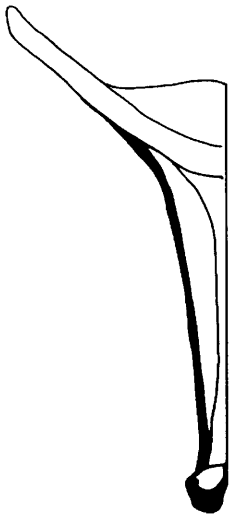


Fig. 10. 36 B

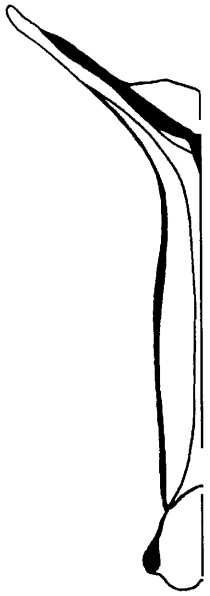


Fig. 10.36 C

Fig. 10.36 D

Fig. 10.36 Dorsal view of metendosternite: A, *Isonychus pictus* B, *Liparetrus lepidopygus* C, *Diphucephala* sp. and D, Melolonthinae sp. 2 (Scarabaeidae: Melolonthinae)

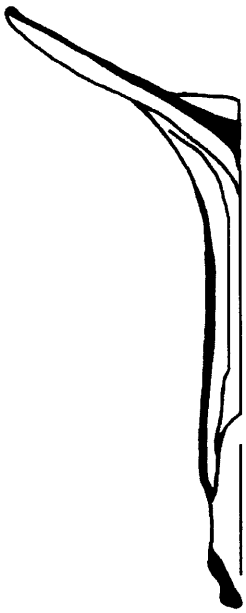


Fig. 10.36 E

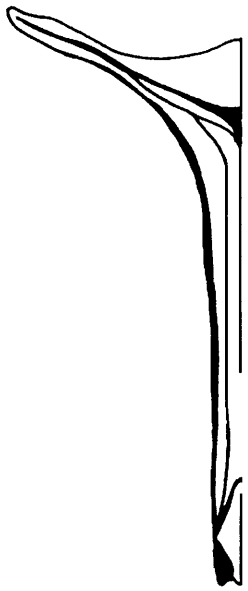


Fig. 10.36 F

Fig. 10.36 G

Fig. 10.36 Frontal view of metendosternite: E, Melolonthinae sp 3; F, Melolonthinae sp. 6 and G, Melolonthinae sp. 7; (Scarabaeidae: Melolonthinae)

Fig. 10.37 A

Fig. 10.37 B

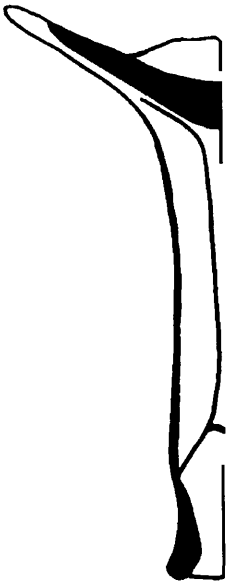


Fig. 10.37 C

Fig. 10.37 Dorsal view of metendosternite: A, Hopliinae sp. 1; B, Hopliinae sp. 2 and C, Hopliinae sp. 3 (Scarabaeidae: Hopliinae)

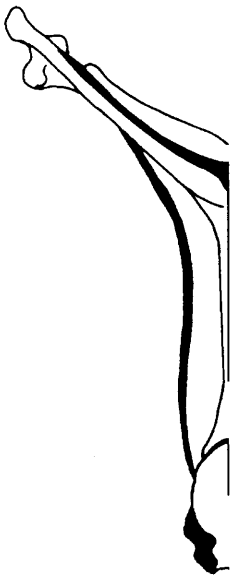


Fig. 10.38 A

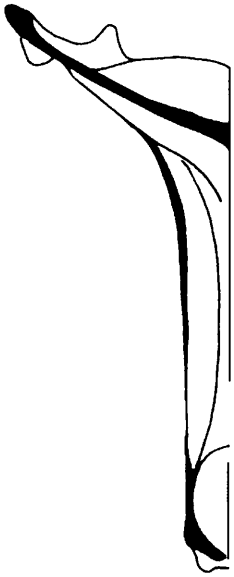


Fig. 10.38 B

Fig. 10.38 C

Fig. 10.38 D

Fig. 10.38 Dorsal view of metendosternite: A, *Anomala daimaina*; B, *Anomala testaceipennis*; C, *Callcodes frenchi* and D, *Stigoderma sulcipennis* (Scarabaeidae: Rutelinae)

Fig. 10.38 E

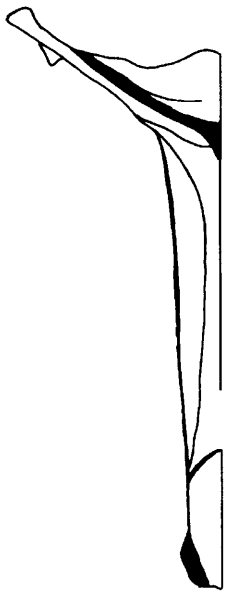


Fig. 10.38 F

Fig. 10. 39 A

Fig. 10.39 B

Fig. 10.38 Dorsal view of metendosternite: E, Rutelinae sp. 1; F, Rutelinae sp. 2 (Scarabaeidae: Rutelinae)

Fig. 10.39 Dorsal view of metendosternite: A, *Heteronychus arator* and B, *Dyscinetus dubius* (Scarabaeidae: Dynastinae)

Fig. 10.39 C

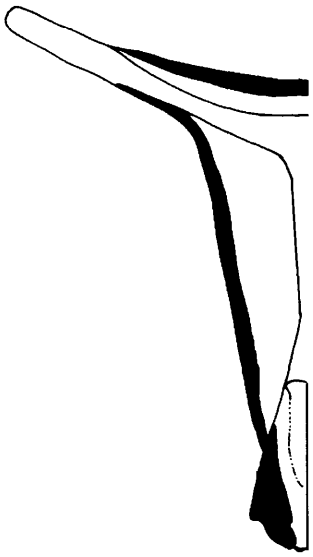


Fig. 10.39 D

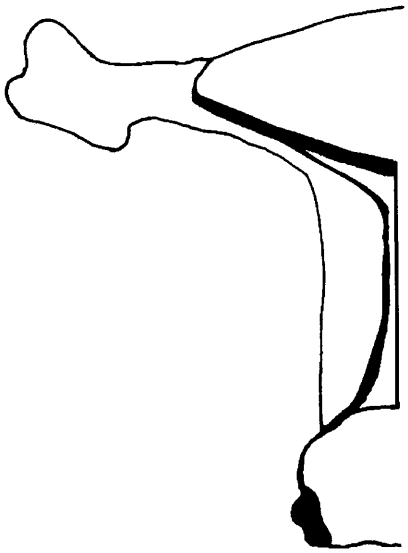


Fig. 10.40 A

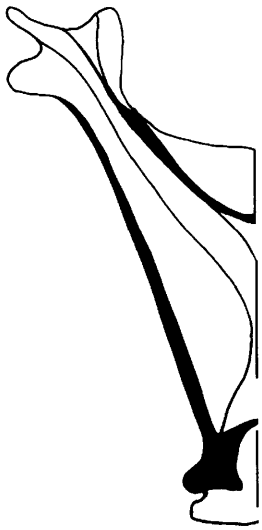


Fig. 10.41 A

Fig. 10. 39 Dorsal view of metendosternite: C, *Aspidolea* sp. and D, Dynastinae sp. 1 (Scarabaeidae: Dynastinae)

Fig. 10.40 Dorsal view of metendosternite: A, *Gnorimella* sp. (Scarabaeidae: Trichiinae)

Fig. 10.41 Dorsal view of metendosternite: A, *Cetonia roelofsi* (Scarabaeidae: Cetoniinae)

Fig. 10.41 B

Fig. 10.41 C

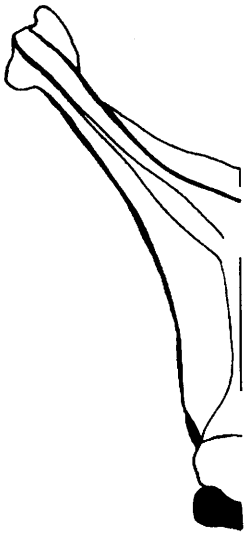


Fig. 10.41 D

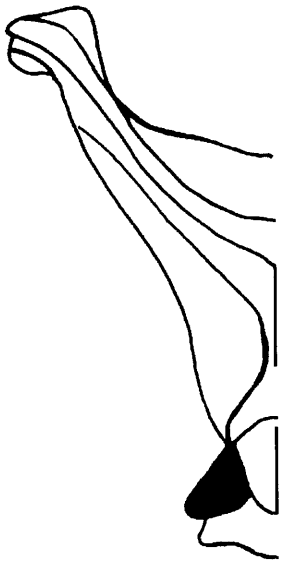


Fig. 10.41 E

Fig. 10.41 Dorsal view of metendosternite: B, *Porphyronota maculatissima*; C, *Hypselogenia geotrupina*, D, *Plaesiorrhinella trivittata* and E, *Diplognatha silicea* (Scarabaeidae: Cetoniinae)

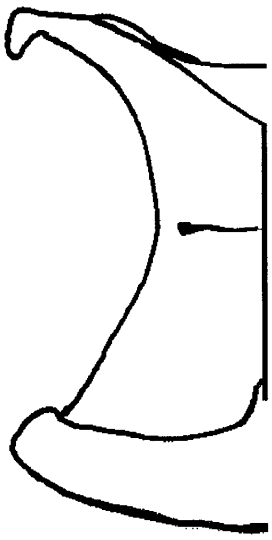


Fig. 10.42 A

Fig. 10.42 Dorsal view of metendosternite: A, Valginae sp. (Scarabaeidae: Valginae)

LATERAL VIEWS OF METENDOSTERNITES

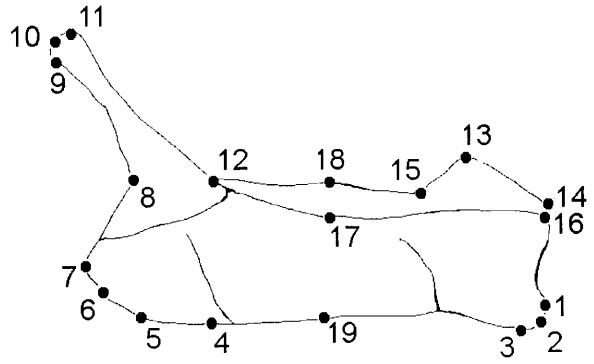


Fig. 10.43 A

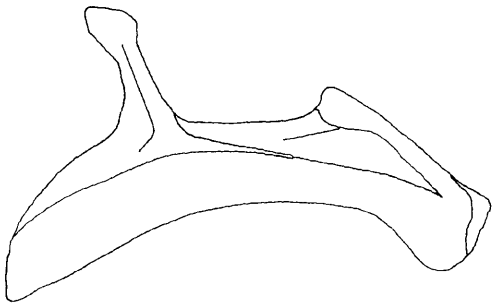


Fig. 10.44 A

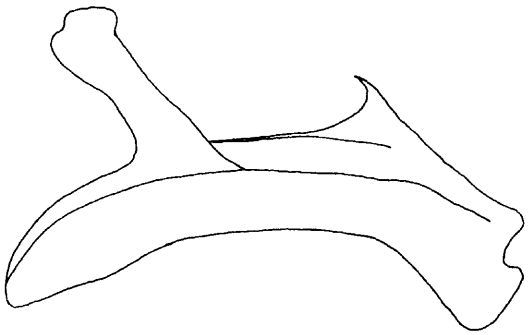


Fig. 10.44 B

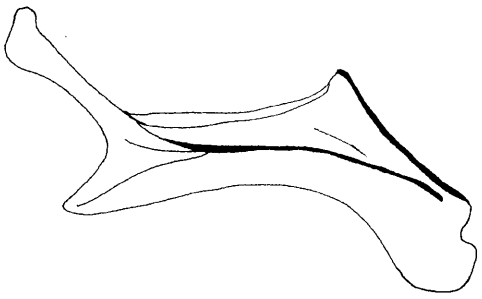


Fig. 10.44 C

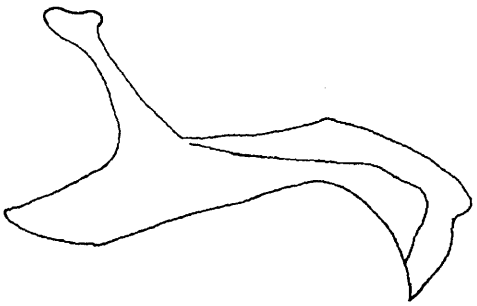


Fig. 10.44 D

Fig. 10.43 Lateral view of metendosternite: A, *Glaresis* sp. (Glaresidae), with landmark positions

Fig. 10.44 Lateral view of metendosternite: A, *Prosopocoilus natalensis*; B, *Macrodorcus rectus*; C, *Nippodorcus rubrofemoratus*; and D, *Syndesus cornutus* (Lucanidae)

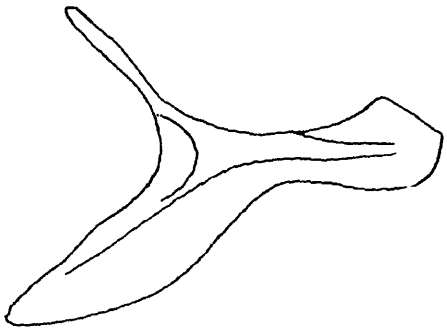


Fig. 10.44 E

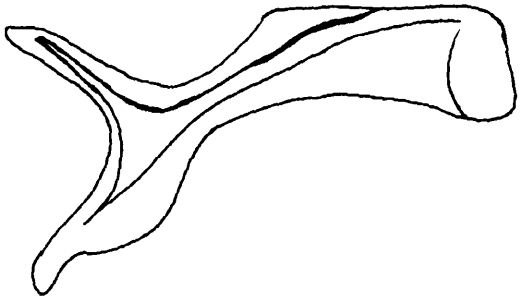


Fig. 10.44 F

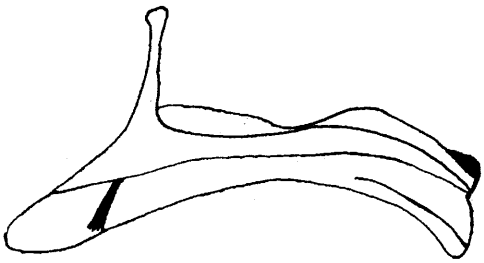


Fig. 10.45 A

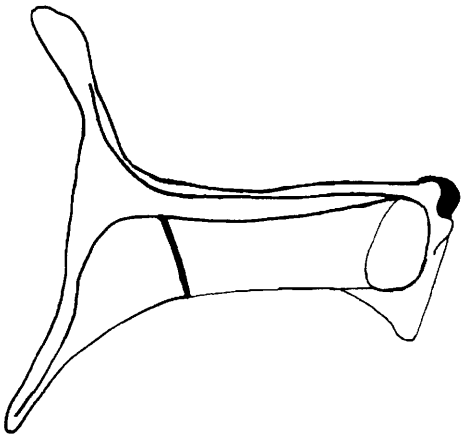


Fig. 10.46 A

Fig 10.44 Lateral view of metendosternite: E, *Sinodendron rugosum* and F, *Ceruchus* sp. (Lucanidae)

Fig. 10.45 Lateral view of metendosternite: A, *Diphyllostoma* sp. (Diphyllostomatidae)

Fig. 10.46 Lateral view of metendosternite: A, *Lichnanthe rathvoni* (Glaphyridae)

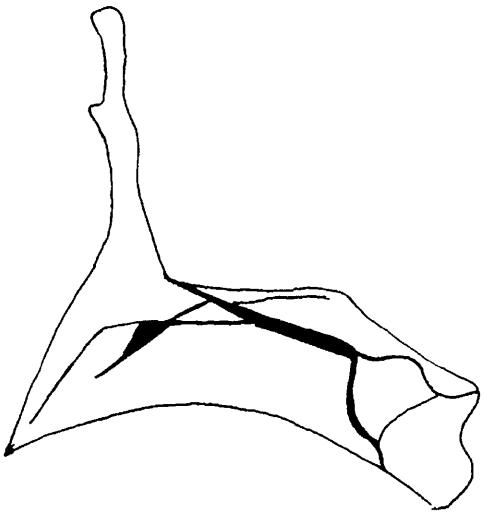


Fig. 10.47 A

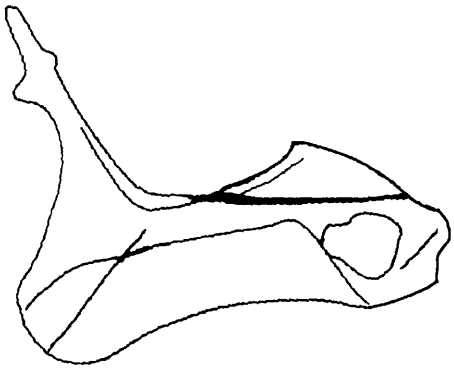


Fig. 10.47 B

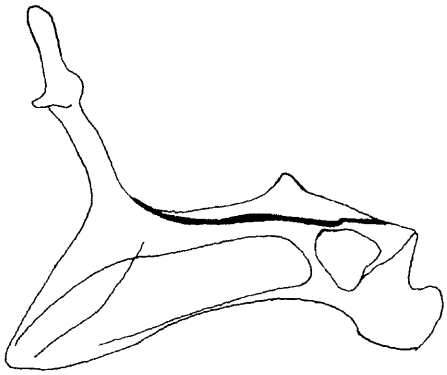


Fig. 10.47 C

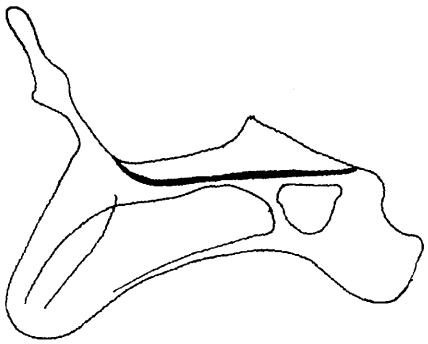


Fig.10.4 D

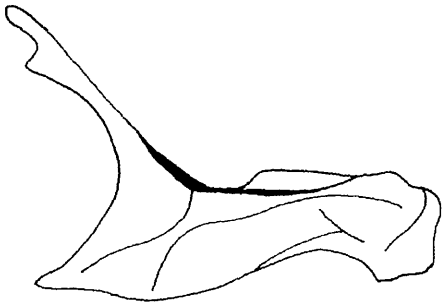


Fig. 10.47 E

Fig. 10.47 Lateral view of metendosternite: A, *Omorgus melancholicus*; B, *Omorgus suberosus*; C, *Omorgus squalidus*; D, *Trox consimilis* and E, *Polynoncus pedestris* (Trogidae)

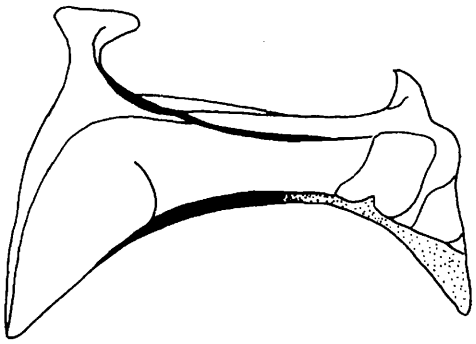


Fig. 10.48 A

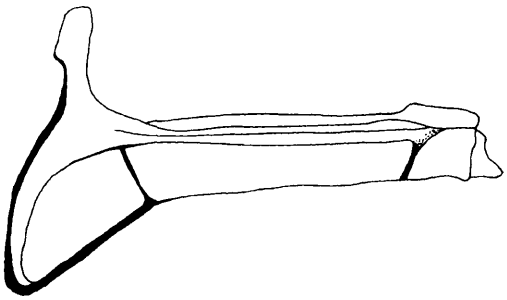


Fig. 10.48 B

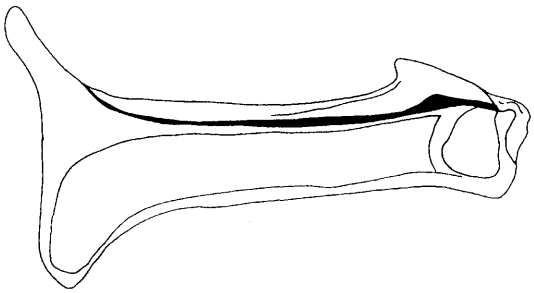


Fig. 10.48 C

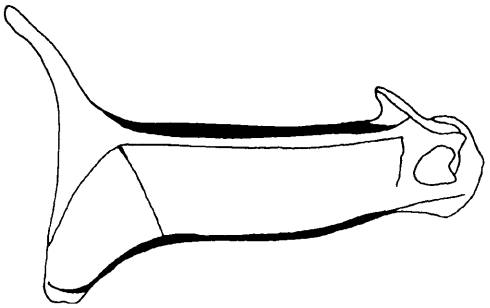


Fig. 10.48 D

Fig. 10.48 Lateral view of Metendosternite: A, *Prototrupes copridoides*; B, *Eucanthus lazarus*; C, *Pseudathyreus orientalis* and D, *Athyreus bifurcatus* (Bolboceratidae)

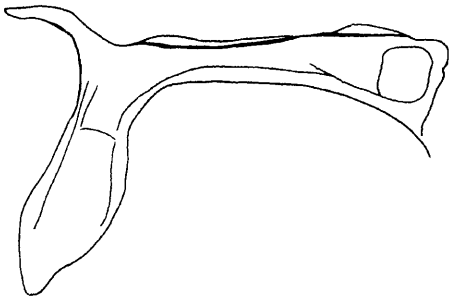


Fig. 10.49 A

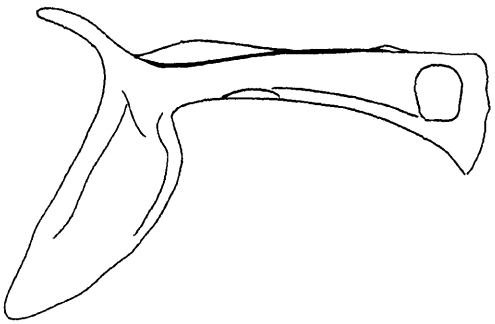


Fig. 10.49 B

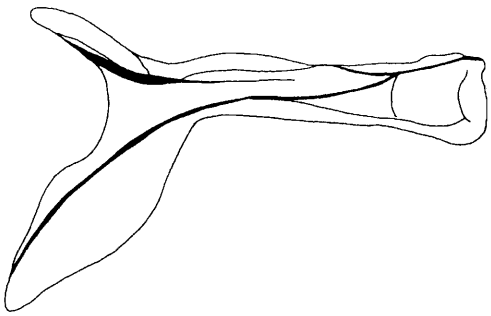


Fig. 10.49 C

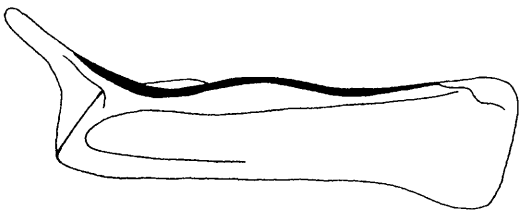


Fig. 10.50 A

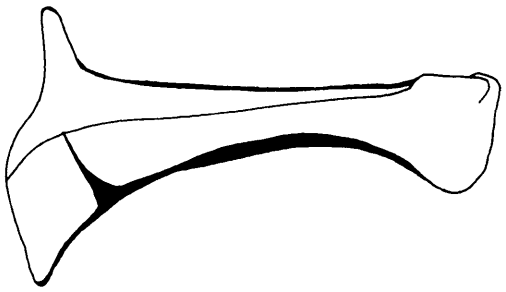


Fig 10.50 B

Fig. 10.49 Frontal view of the metendosternite: A, *Pleocoma shostensis;* B, *Pleocoma simbriata* and C, *Pleocoma* sp (Pleocomidae)

Fig. 10.50 Lateral view of the metendosternite: A, T*aurocerastes* sp. and B, *Geotrupes spiniger* (Geotrupidae)

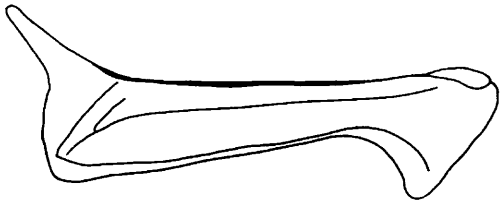


Fig. 10.50 C

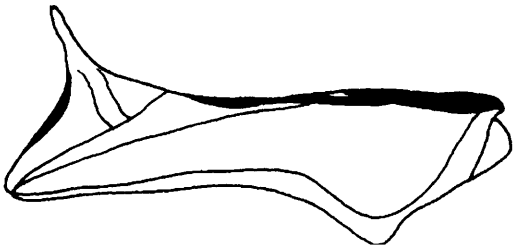


Fig. 10.50 D

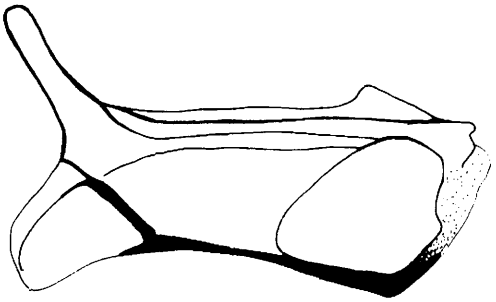


Fig. 10.51 A

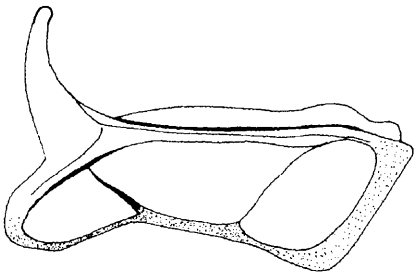


Fig. 10.51 B

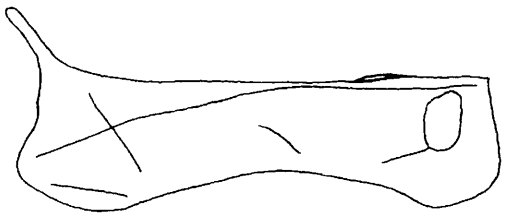


Fig. 10.51 C

Fig. 10.52 A

Fig 10.50 Lateral view of the metendosternite; C, *Thorectus cheisinus* and D, *Lethrus carinatus* (Geotrupidae)

Fig. 10.51 Lateral view of metendosternite: A, *Ochodaeus kansasus*; B, *Ochodaeus repondus* and C, *Synochodaeus cucullus* (Ochodaeidae)

Fig. 10.52 Lateral view of metendosternite: A, Ceratocanthidae sp. (Ceratocanthidae)

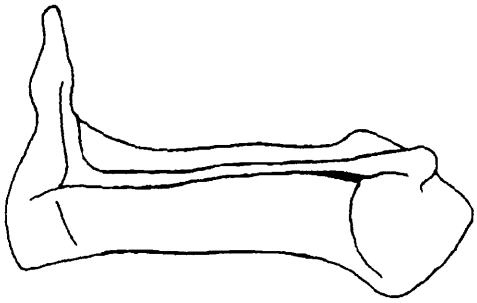


Fig. 10.53 A

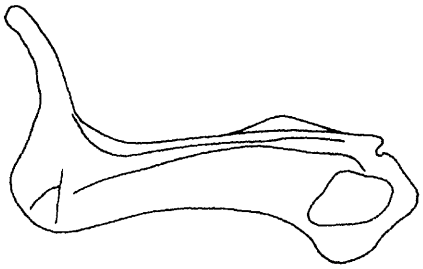


Fig. 10.53 B

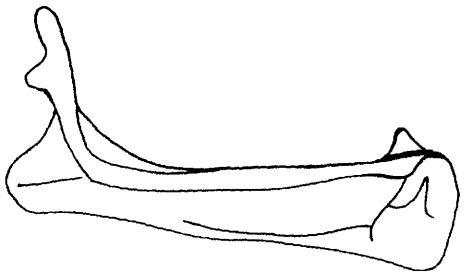


Fig. 10.53 C

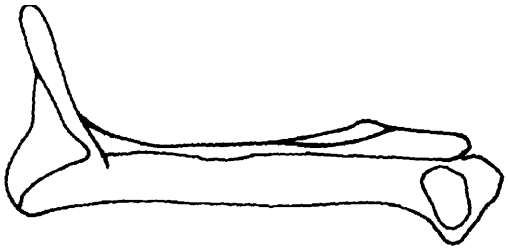


Fig. 10.53 D

Fig. 10.53 Lateral view of metendosternite: A, *Phaeochrous mashunus;* B, *Hybosorus illegri,* C, *Liparochrus fossulatus* and D, *Coelodus cataneus* (Hybosoridae)

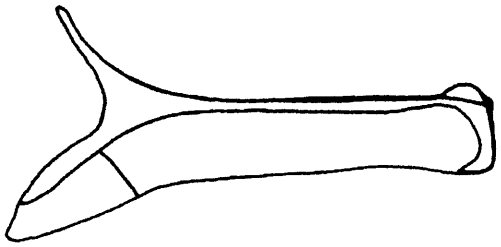


Fig. 10. 54 A

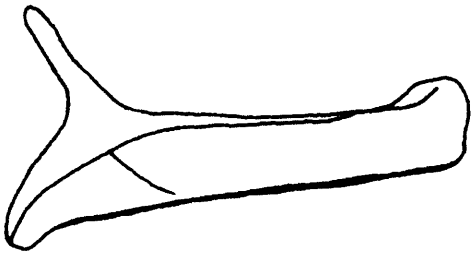


Fig. 10.54 B

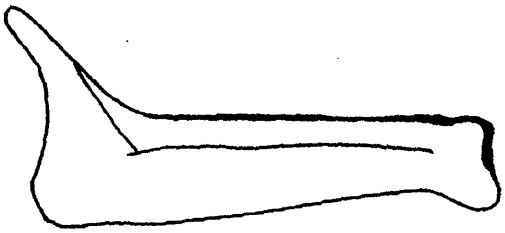


Fig. 10.54 C

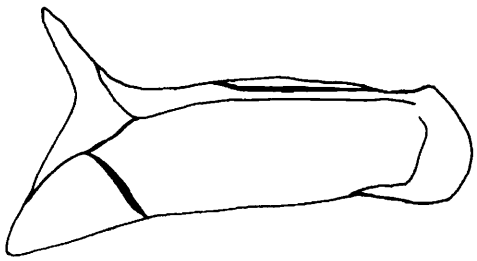


Fig. 10.54 D

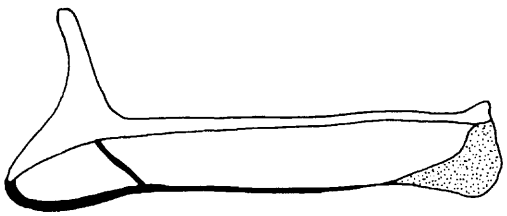


Fig. 10.54 E

Fig. 10.54 F

Fig. 10.54 Frontal view of metendosternite: A, *Aphodius russatus*; B, *Aphodius septemmaculatus,* C, *Aphodius porcus;* D, *Colobopterus maculecollis;* E, *Pseudaphodius rufiventris* and F, *Ataenius alternatus* (Scarabaeidae: Aphodiinae)

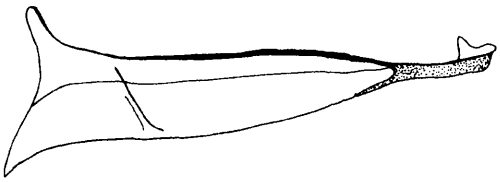


Fig. 10.55 A

Fig. 10.55 B

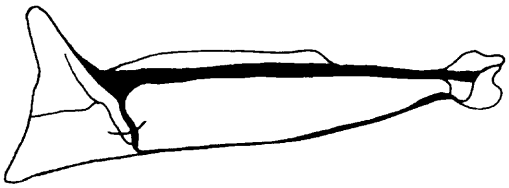


Fig. 10.55 C

Fig. 10.55 D

Fig. 10.55 E

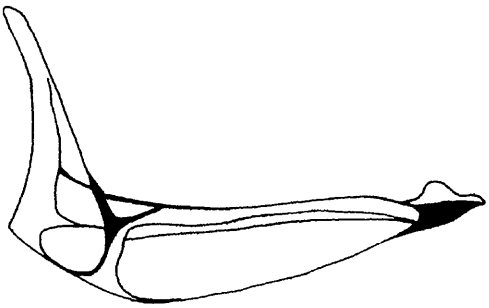


Fig. 10.55 F

Fig. 10.55 Lateral view of metendosternite: A, *Onthophagus ferrox;* B, *Sisyphus* sp.; C, *Kheper* sp.; D, *Circellium bacchus*; E, Coprini sp. and F, *Cephalodesmius armiger* (Scarabaeidae: Scarabaeinae)

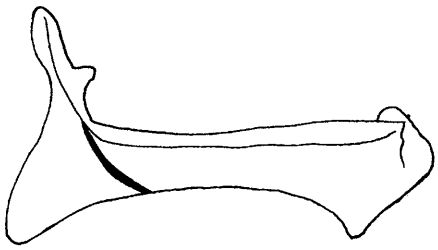


Fig. 10.56 A

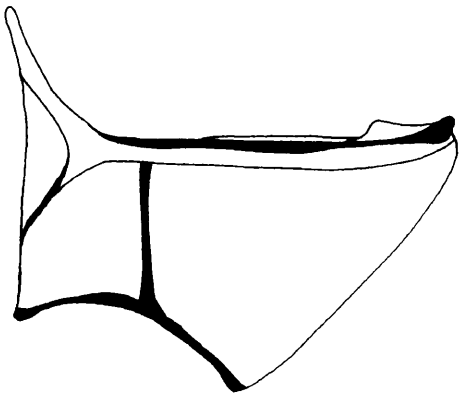


Fig. 10.57 A

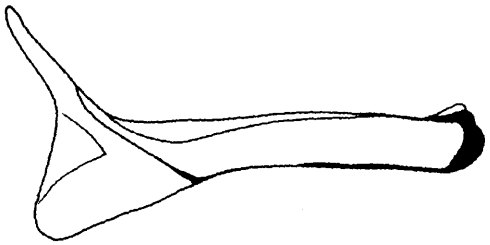


Fig. 10.57 B

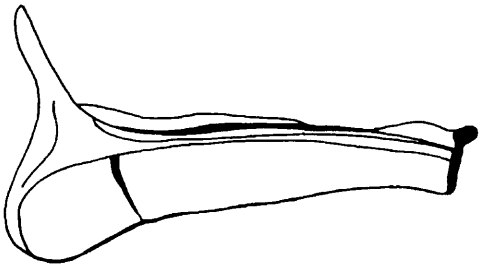


Fig. 10.57 C

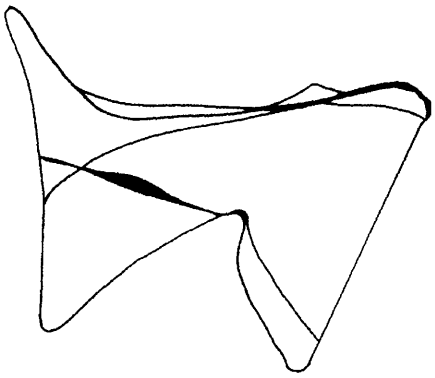


Fig. 10.57 D

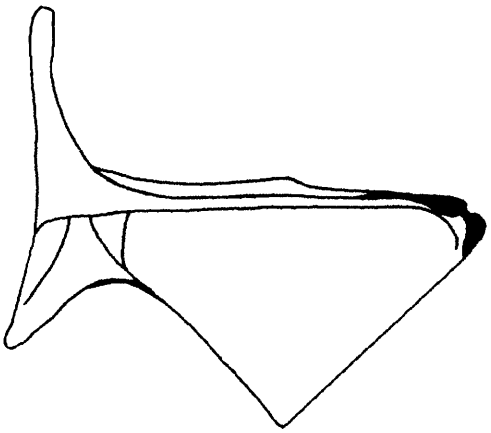


Fig. 10.57 E

Fig. 10.56 Lateral view of metendosternite: A, *Orphnus capensis* (Scarabaeidae: Orphninae)

Fig. 10.57 Lateral view of metendosternite: A, *Isonychus pictus* B, *Liparetrus lepidopygus* ;C, *Diphucephala* sp.; D, Melolonthinae sp. 2 and Melolonthinae sp. 3 (Scarabaeidae: Melolonthinae)

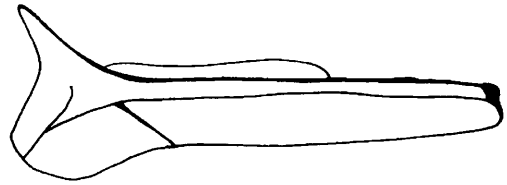


Fig. 10.57 F

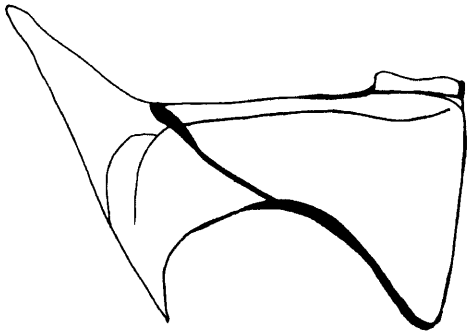


Fig. 10.58 A

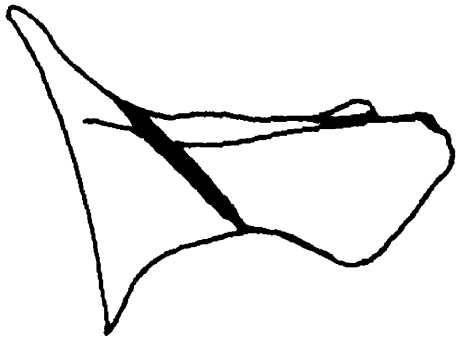


Fig. 10.58 B

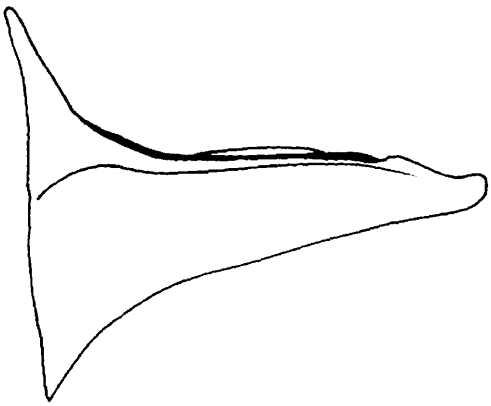


Fig. 10.58 C

Fig. 10.57 Lateral view of metendosternite: F, Melolonthinae sp 6 (Scarabaeidae: Melolonthinae)

Fig. 10.58 Lateral view of metendosternite: A, Hopliinae sp. 1; B, Hopliinae sp. 2 and C, Hopliinae sp. 3 (Scarabaeidae: Hopliinae)

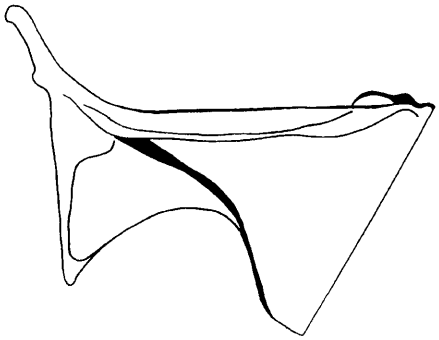


Fig. 10.59 A

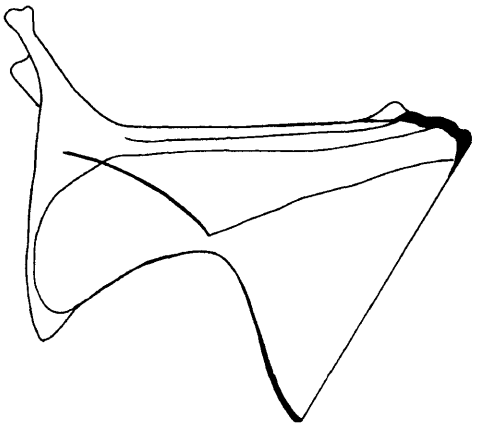


Fig. 10.59 B

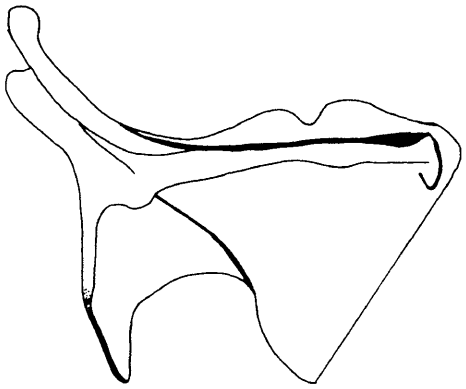


Fig. 10.59 C

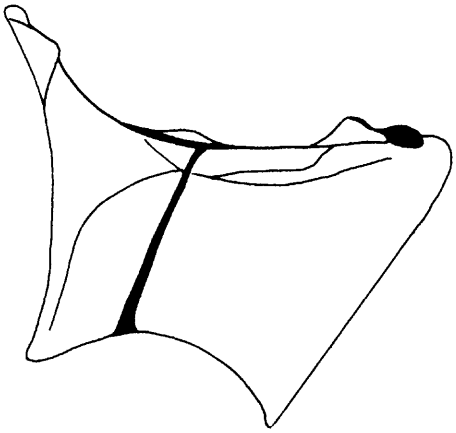


Fig. 10.59 D

Fig. 10.59 Lateral view of metendosternite: A, *Anomala daimaina*; B, *Anomala testaceipennis; C, Callcodes frenchi;* D, *Stigoderma sulcipennis*.

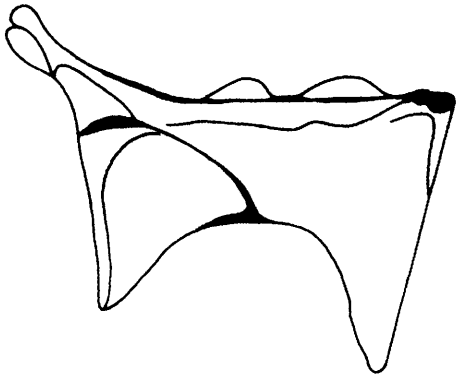


Fig. 10.59 E

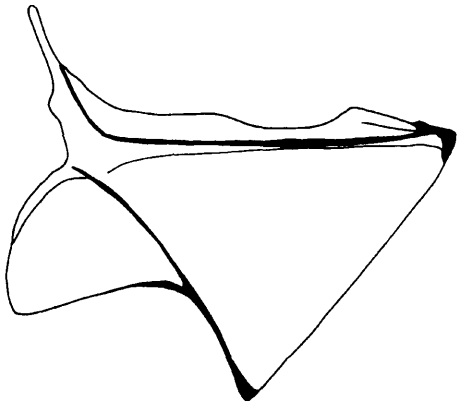


Fig. 10.59 F

Fig. 10.59 Lateral view of metendosternite: E, Rutelinae sp. 1 and F, Rutelinae sp. 2 (Scarabaeidae: Rutelinae)

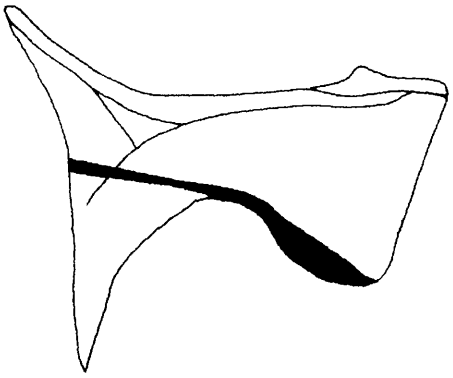


Fig. 10.60 A

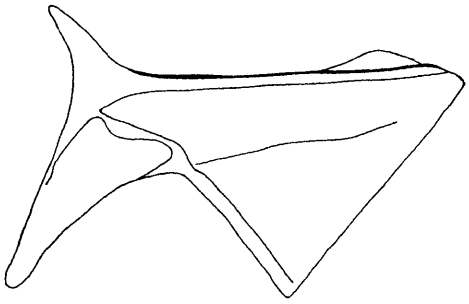


Fig. 10.60 B

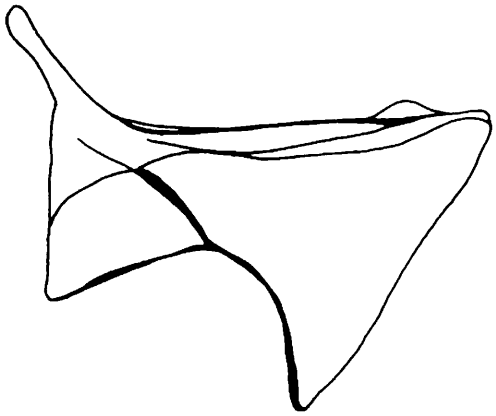


Fig.10.60 C

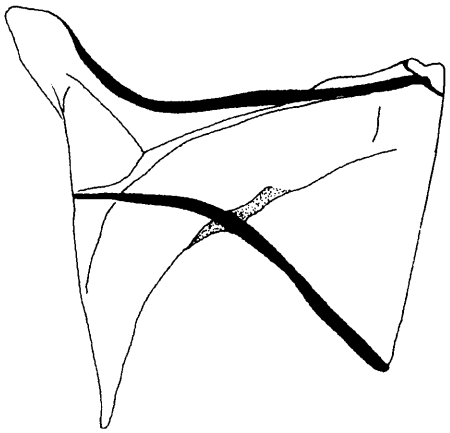


Fig. 10.60 D

Fig. 10.60 Lateral view of metendosternite: A, *Heteronychus arator* ; B, *Dyscinetus dubius;* C, *Aspidolea* sp. and D, Dynastinae sp. 1 (Scarabaeidae: Dynastinae)

Fig. 10.61 A

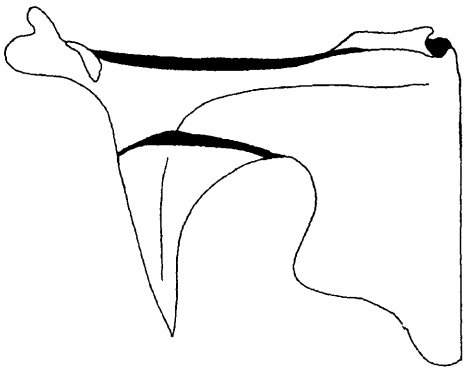


Fig. 10.61 B

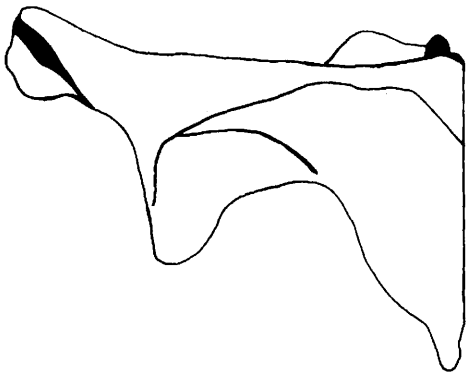


Fig. 10.61 C

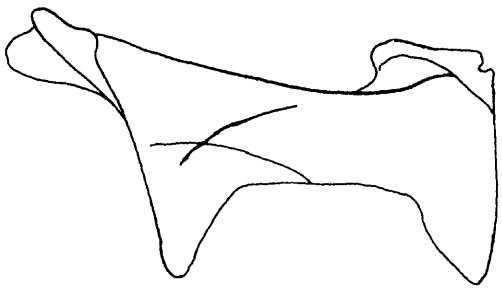


Fig. 10.61 D

Fig. 10.61 Lateral view of metendosternite: A, *Cetonia roelofsi* ; B; *Hypselogenia geotrupina*; C, *Diplognatha silicea* and D, *Eudicella smithii* (Scarabaeidae: Cetoniinae)

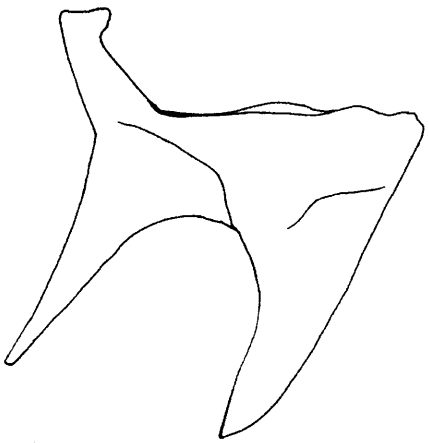


Fig. 10.62 A

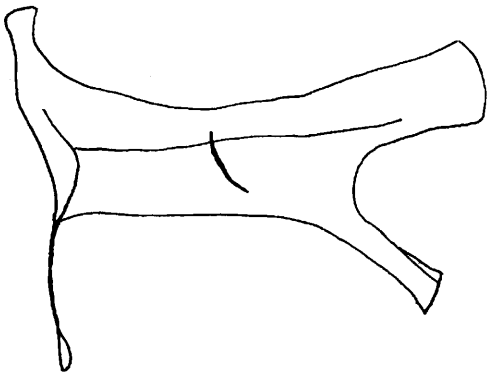


Fig. 10.63 A

Fig. 10.62 Lateral view of metendosternite: A, *Gnorimella* sp. (Scarabaeidae: Trichiinae)

Fig. 10.63 Lateral view of metendosternite: A, Valginae sp. (Scarabaeidae: Valginae)

DETERMINING WHETHER AMOUNT OF VARIATION IS SMALL ENOUGH FOR STATISTICAL ANALYSIS

The correlation (uncentered) between the tangent space, Y, regressed onto Procrustes distance (geodesic distances in radians) for the frontal view data set is 0.999987; dorsal view is 1.000000 and the lateral view is 0.999994. The scatters for all three data sets are nearly perfect, implying that the approximation is good enough for these data.

DETERMINING THE CONSENSUS CONFIGURATION FOR EACH TAXON

Figures 10.64 to 10.126 indicate consensus configurations of different taxa examined. In cases where a single species was used, only landmark positions are provided because it was not possible to compute a mean consensus configuration for the taxon. The landmarks of the single species were, therefore, taken as representative consensus configurations for the taxon. Consensus configurations of the individual subfamilies of the Scarabaeidae were computed, where after a consensus configuration of the family was computed using the consensus configurations of the individual subfamilies.

Metendosternite morphology of members of the same taxa shows very little variation in all three views. There are however small differences – this is ascribed to within species variation. If the consensus configuration for each taxon is therefore compared to the individual landmark positions of the members of the specific taxon, little deviations are present. The consensus configuration for the Scarabaeidae (the most derived family) was compiled by using the landmark positions of the consensus configurations of all the members of the subfamilies The landmark positions of the consensus configuration of the Scarabaeidae deviate more from the individual subfamily consensus configurations; this is especially clear in the lateral views. The more primitive members of the Scarabaeidae (e.g. Aphodiinae and Scarabaeinae) have a flatter ventral rib, while the more derived members (Rutelinae, Cetoniinae etc.) possess a wider ventral rib. In the consensus configuration of the family, this wider ventral rib is seen. A clear pattern can already be noted by examining the consensus configurations of the different taxa.

RESULTS OF THE CONSENSUS CONFIGURATION OF THE FRONTAL VIEWS OF THE METENDOSTERNITES OF THE SCARABAEOIDEA TAXA

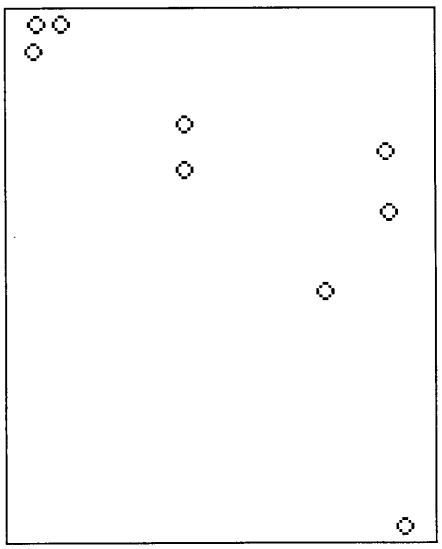


Fig. 10.64 Lucanidae

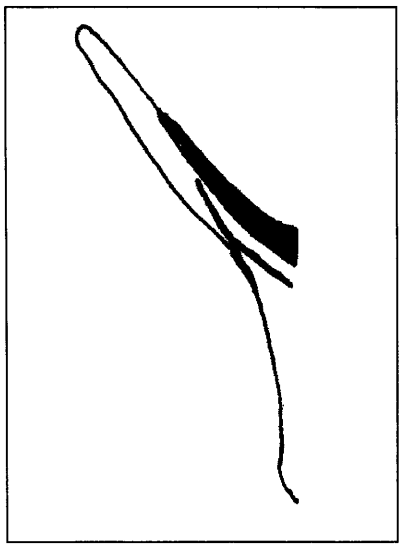


Fig 10.65 Diphylostomatidae

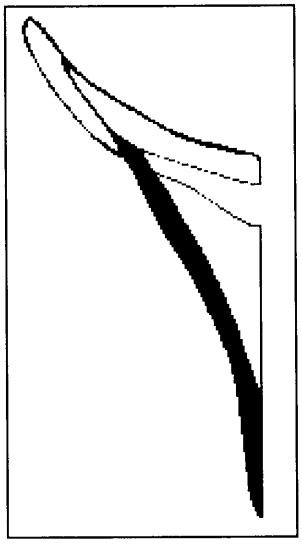


Fig. 10.66 Glaphyridae

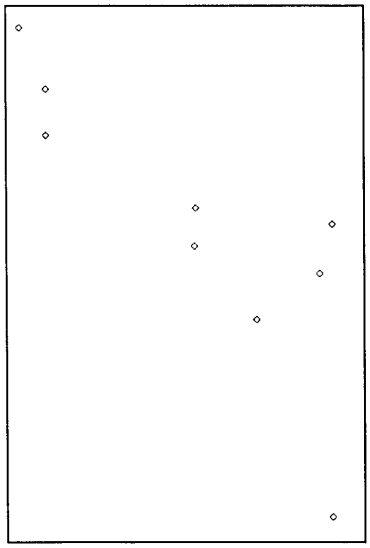


Fig. 10.67 Trogidae

Fig. 10.64 Consensus configuration of landmarks of all studied species of Lucanidae; **Fig. 10.65:** Landmark positions single species of Diphyllostomatidae; **Fig. 10.66** Landmark positions single species of Glaphyridae; **Fig 10.67** Consensus configuration of landmarks of all studied species of Trogidae.

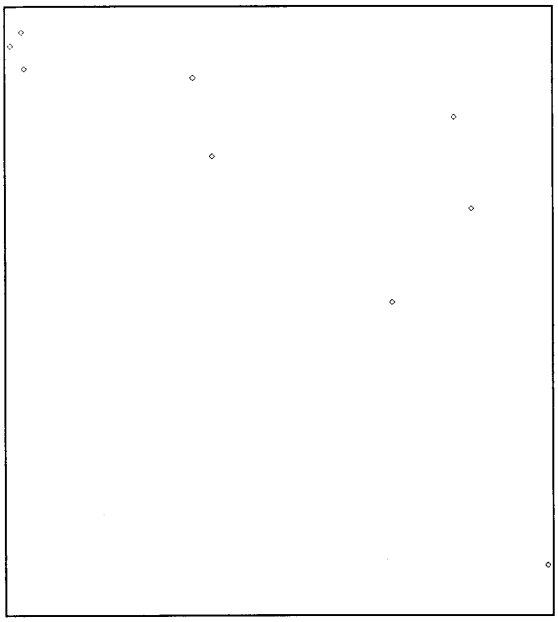


Fig. 10.68 Bolboceratidae

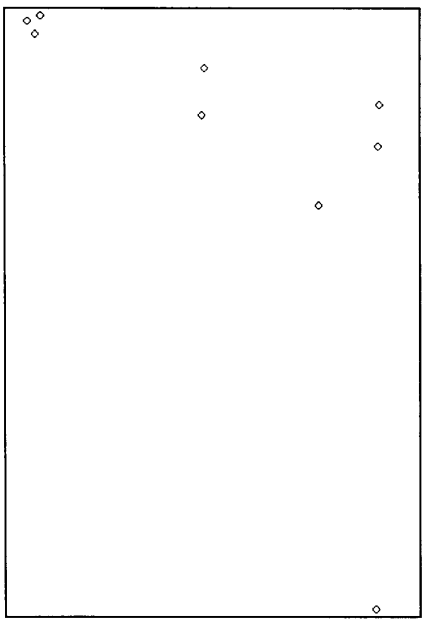


Fig 10.69 Pleocomidae

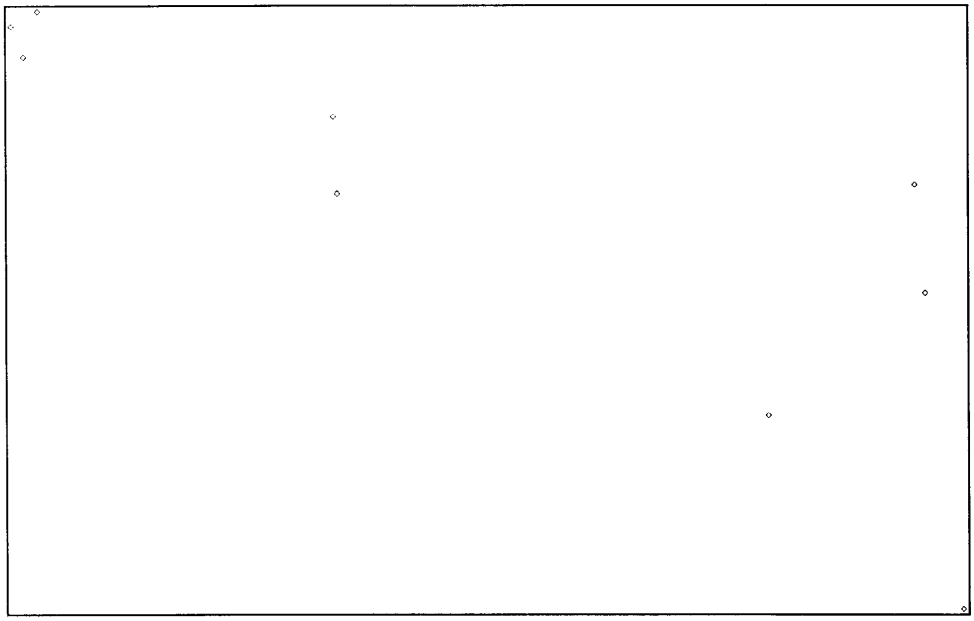


Fig 10.70 Geotrupidae

Fig. 10.68 Consensus configuration of landmarks of all studied species of Bolboceratidae; **Fig 10.69** Consensus configuration of landmarks of all studied species of Pleocomidae; **Fig. 10.70** Consensus configuration of landmarks of all studied species of Geotrupidae.

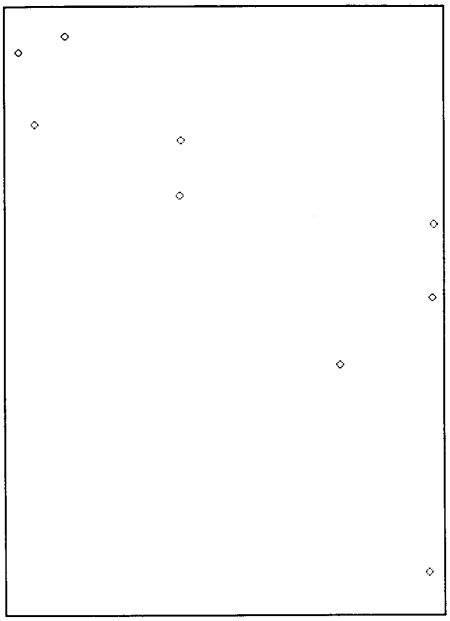


Fig 10.71 Ochodaeidae

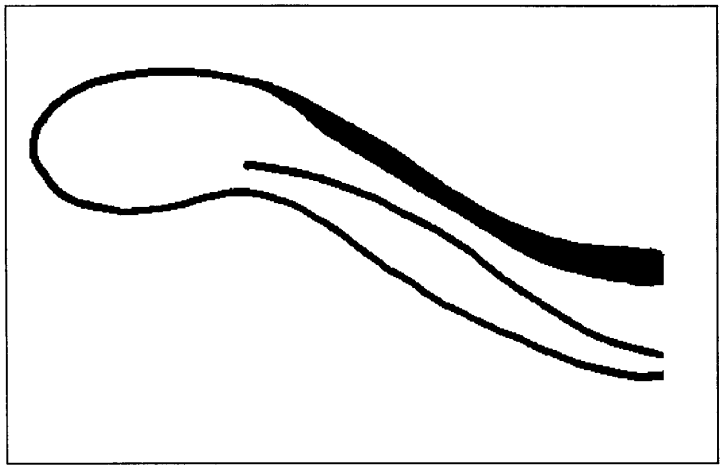


Fig 10.72 Ceratocanthidae

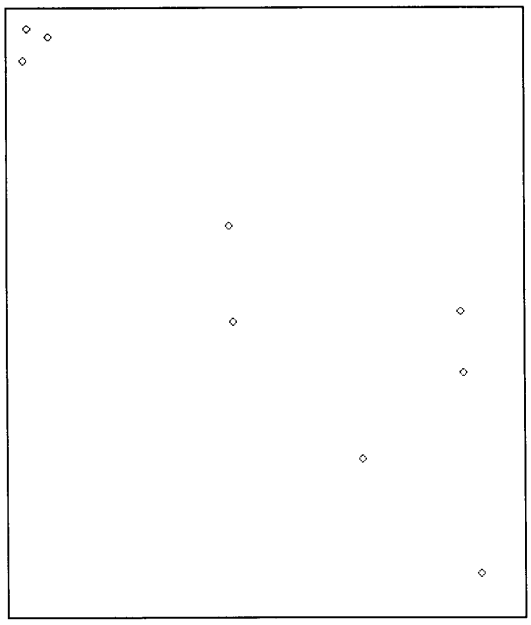


Fig. 10.73 Hybosoridae

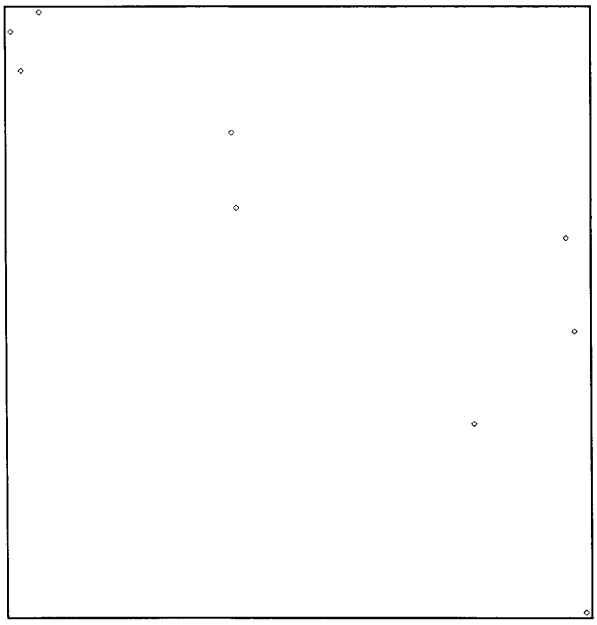


Fig. 10.75 Scarabaeidae: Aphodiinae

Fig. 10.71 Consensus configuration of landmarks of all studied species of Ochodaeidae; **Fig. 10.72** Landmark positions of single species of Ceratocanthidae studied; **Fig. 10.73** Consensus configuration of landmarks of all studied species of Hybosoridae; **Fig. 10.74** Consensus configuration of landmarks of all studied species of Aphodiinae (Scarabaeidae)

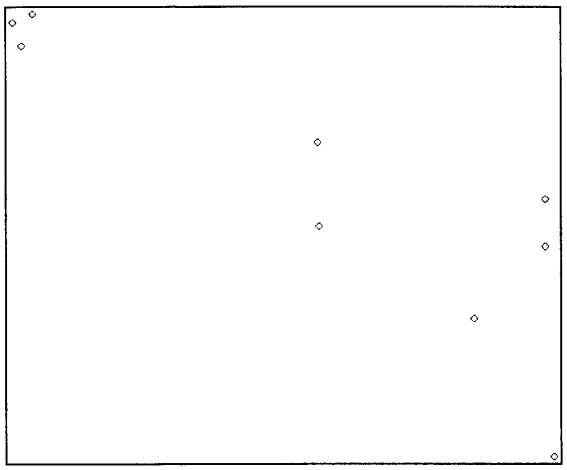


Fig. 10.75 Scarabaeidae: Scarabaeinae

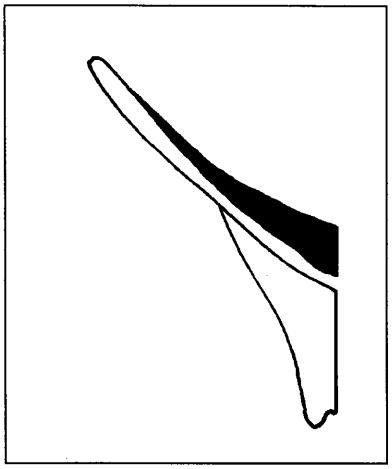


Fig. 10.76: Scarabaeidae: Orphninae

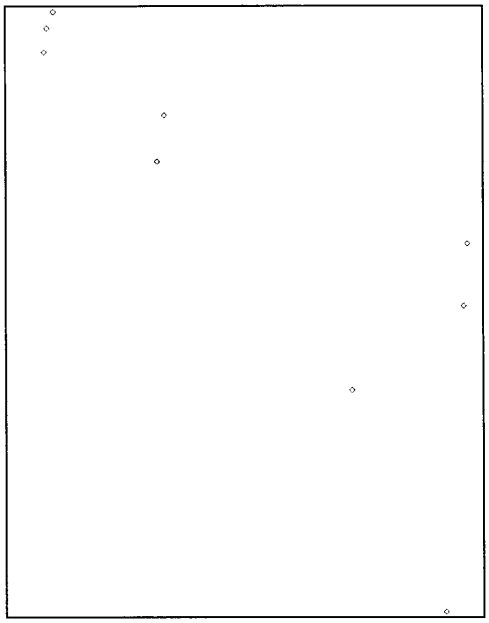


Fig. 10.77 Scarabaeidae: Melolonthinae

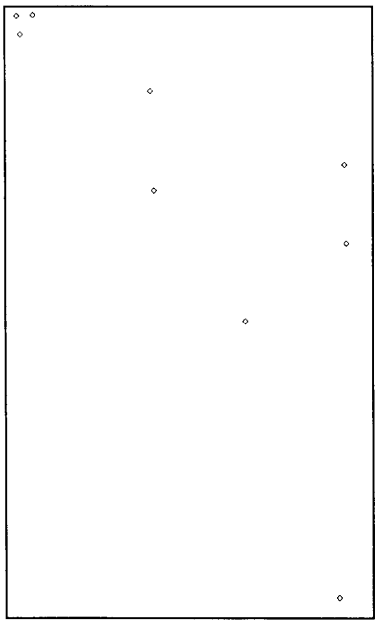


Fig. 10.78 Scarabaeidae: Hopliinae

Fig. 10.75 Consensus configuration of landmarks of all studied species of Scarabaeinae (Scarabaeidae); **Fig. 10.76** Landmark positions of single species of Orphninae (Scarabaeidae) studied; **Fig. 10.77** Consensus configuration of landmarks of all studied species of Melolonthinae (Scarabaeidae); **Fig. 10.78** Consensus configuration of landmarks of all studied species of Hopliinae (Scarabaeidae)

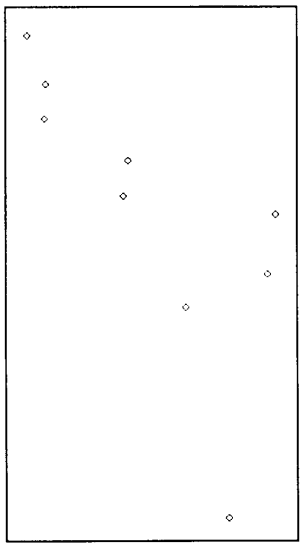


Fig. 10.79 Scarabaeidae: Rutelinae

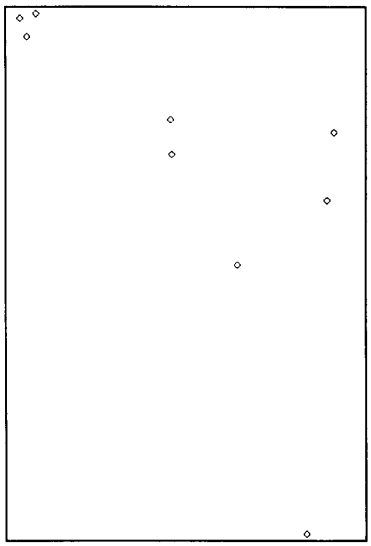


Fig. 10.80 Scarabaeidae: Dynastinae

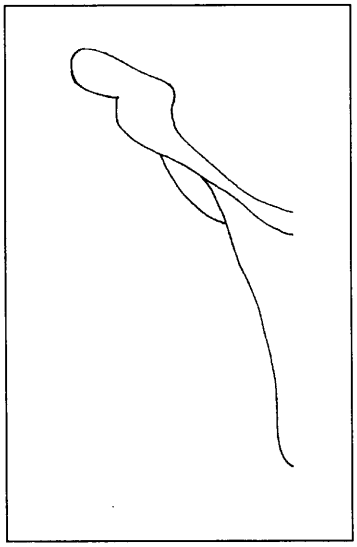


Fig. 10.81 Scarabaeidae: Trichiinae

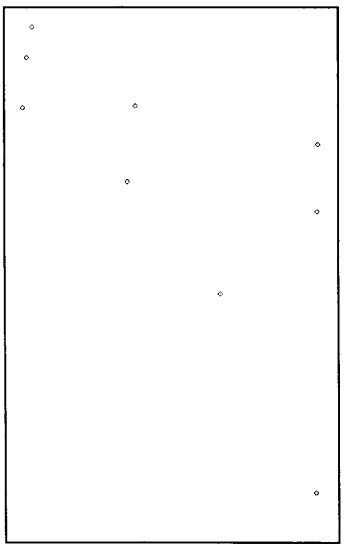


Fig. 10.82 Scarabaeidae: Cetoniinae

Fig. 10.79 Consensus configuration of landmarks of all studied species of Rutelinae (Scarabaeidae); **Fig. 10.80** Consensus configuration of landmarks of all studied species of Dynastinae (Scarabaeidae); **Fig. 10.81** Landmark positions of single species studied of Trichiinae (Scarabaeidae); **Fig. 10.82** Consensus configuration of landmarks of all studied species of Cetoniinae (Scarabaeidae).

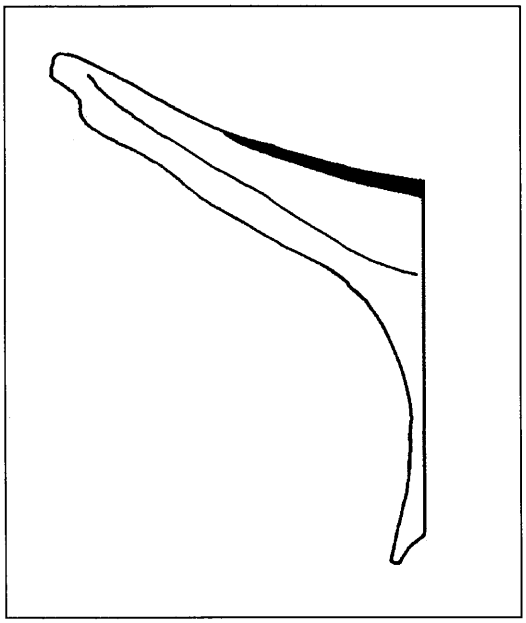


Fig. 10.83 Scarabaeidae: Valginae

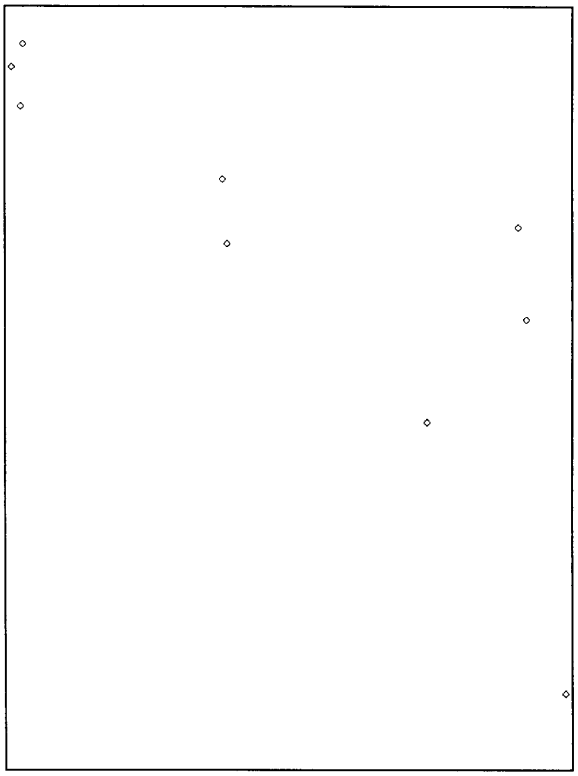


Fig. 10.84 Scarabaeidae

Fig. 10.83 Landmark positions of single species studied of Valginae (Scarabaeidae); **Fig. 10.84** Consensus configuration of landmarks of Scarabaeidae compiled from consensus configurations all subfamilies studied.

RESULTS OF THE CONSENSUS CONFIGURATION OF THE DORSAL VIEWS OF THE METENDOSTERNITES OF THE SCARABAEOIDEA TAXA

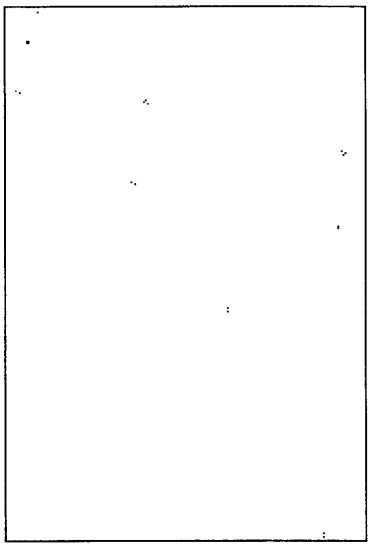


Fig. 10.85 Lucanidae

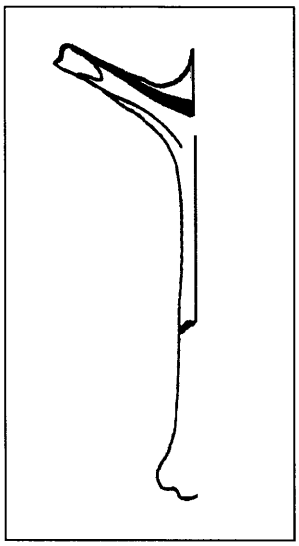


Fig. 10.86 Diphyllostomatidae

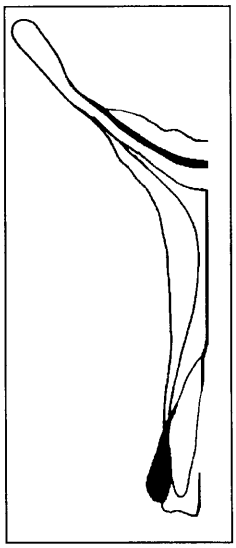


Fig. 10.87 Glaphyridae

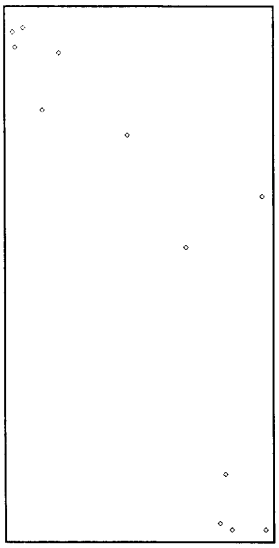


Fig. 10.88 Trogidae

Fig. 10.85 Consensus configuration of landmarks of all studied species of Lucanidae; **Fig. 10.86** Landmark positions single species of Diphyllostomatidae; **Fig. 10.87** Landmark positions single species of Glaphyridae; **Fig 10.88** Consensus configuration of landmarks of all studied species of Trogidae.

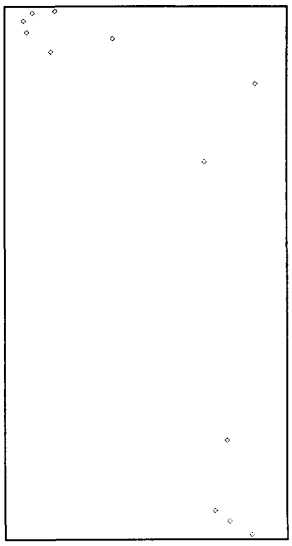


Fig. 10.89 Bolboceratidae

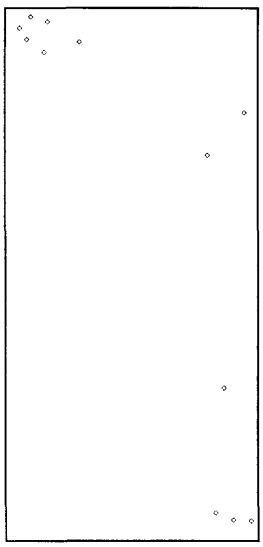


Fig. 10.90 Pleocomidae

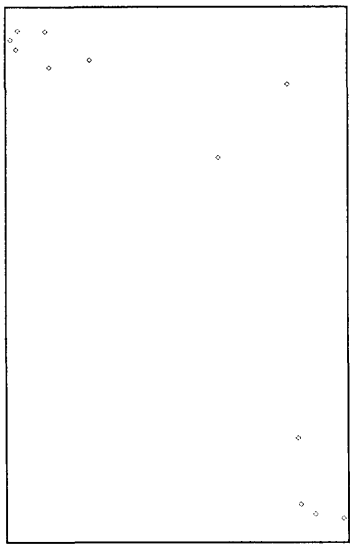


Fig. 10.91 Geotrupidae

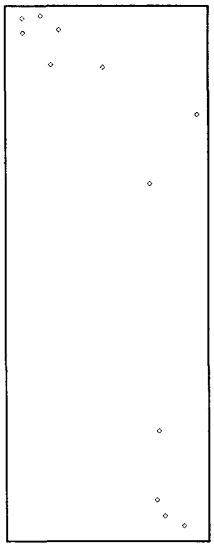


Fig. 10. 92 Ochodaeidae

Fig. 10.89 Consensus configuration of landmarks of all studied species of Bolboceratidae; **Fig 10.90** Consensus configuration of landmarks of all studied species of Pleocomidae; **Fig. 10.91** Consensus configuration of landmarks of all studied species of Geotrupidae; **Fig. 10.92** Consensus configuration of landmarks of all studied species of Ochodaeidae.

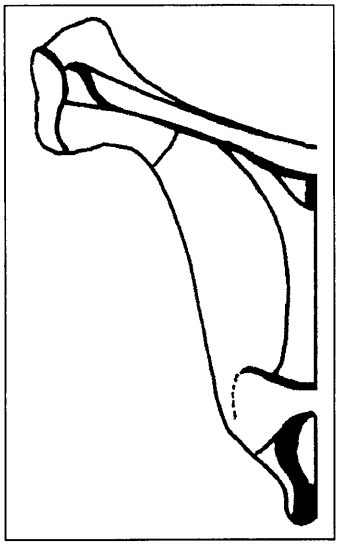


Fig. 10.93 Ceratocanthidae

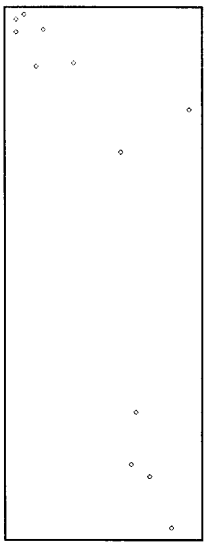


Fig. 10.94 Hybosoridae

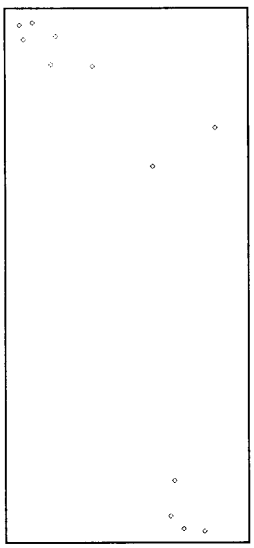


Fig. 10. 95 Scarabaeidae: Aphodiinae

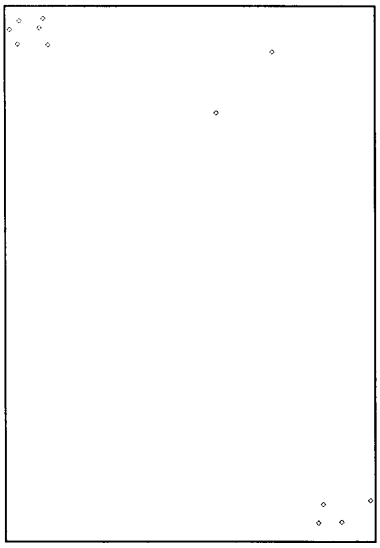


Fig. 10.96 Scarabaeidae: Scarabaeinae

Fig. 10.93 Landmark positions of single species of Ceratocanthidae studied; **Fig. 10.94** Consensus configuration of landmarks of all studied species of Hybosoridae; **Fig. 10.95** Consensus configuration of landmarks of all studied species of Aphodiinae (Scarabaeidae); **Fig. 10.96** Consensus configuration of landmarks of all studied species of Scarabaeinae (Scarabaeidae).

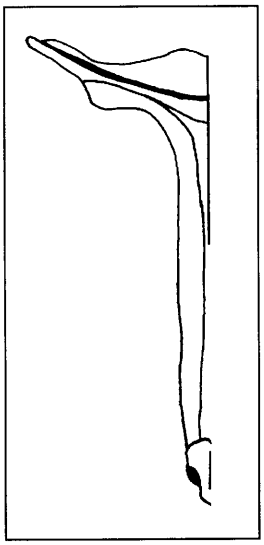


Fig. 10.97 Scarabaeidae: Orphninae

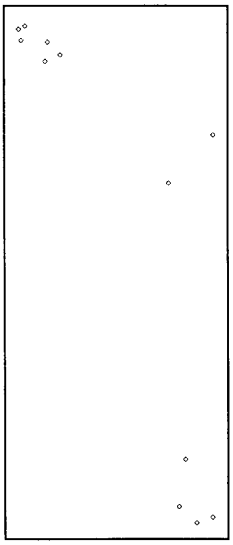


Fig. 10. 98 Scarabaeidae: Melolonthinae

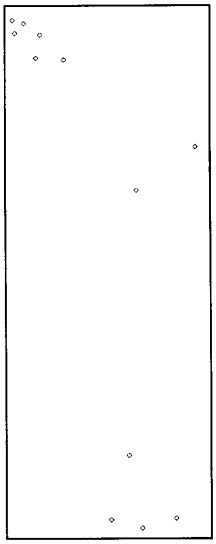


Fig. 10.99 Scarabaeidae: Hopliinae

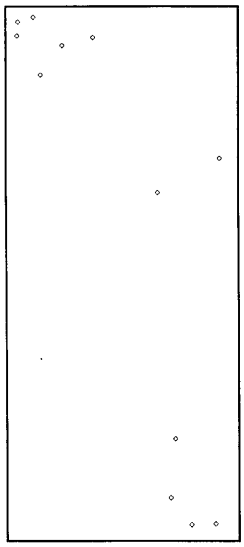


Fig. 10.100 Scarabaeidae: Rutelinae

Fig. 10.97 Landmark positions of single species of Orphninae (Scarabaeidae) studied; **Fig. 10.98** Consensus configuration of landmarks of all studied species of Melolonthinae (Scarabaeidae); **Fig. 10.99** Consensus configuration of landmarks of all studied species of Hopliinae (Scarabaeidae); **Fig. 10.100** Consensus configuration of landmarks of all studied species of Rutelinae (Scarabaeidae).

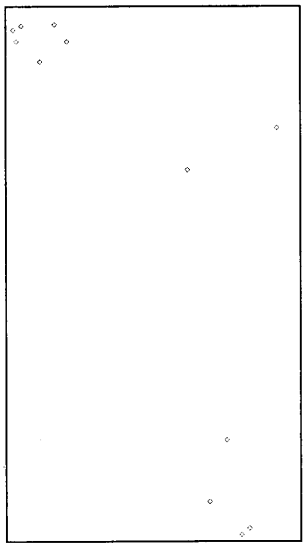


Fig. 10.101 Scarabaeidae: Dynastinae

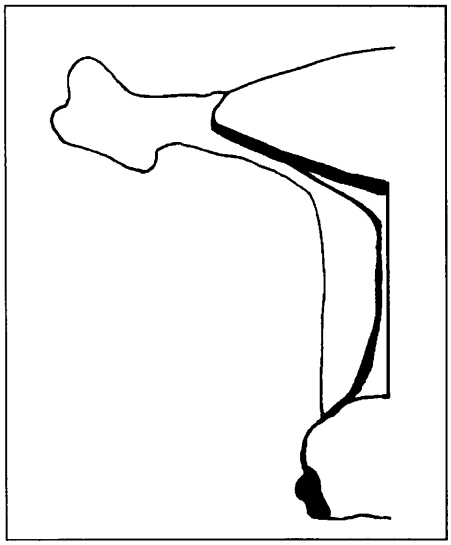


Fig. 10.102 Scarabaeidae: Trichiinae

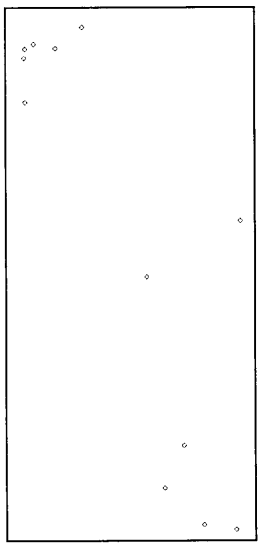


Fig. 10.103 Scarabaeidae: Cetoniinae

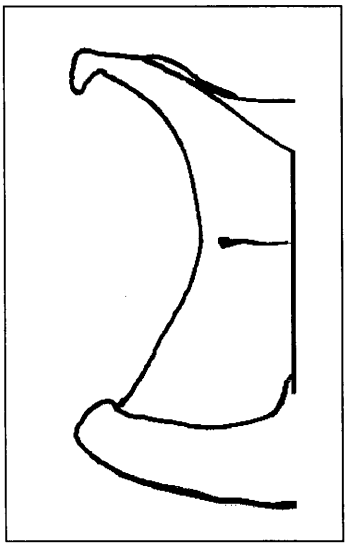


Fig. 10.104 Scarabaeidae: Valginae

Fig. 10.101 Consensus configuration of landmarks of all studied species of Dynastinae (Scarabaeidae); **Fig. 10.102** Landmark positions of single species studied of Trichiinae (Scarabaeidae); **Fig. 10.103** Consensus configuration of landmarks of all studied species of Cetoniinae (Scarabaeidae); **Fig. 10.104** Landmark positions of single species studied of Valginae (Scarabaeidae).

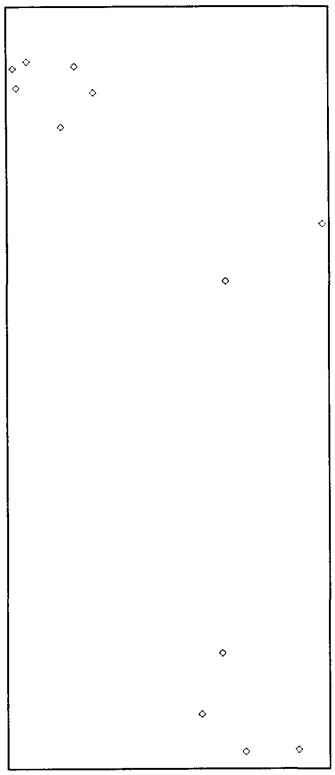


Fig 10.105: Scarabaeidae

Fig. 10.105 Consensus configuration of landmarks of Scarabaeidae compiled from consensus configurations all subfamilies studied.

RESULTS OF THE CONSENSUS CONFIGURATION OF THE LATERAL VIEWS OF THE METENDOSTERNITES OF THE SCARABAEOIDEA TAXA

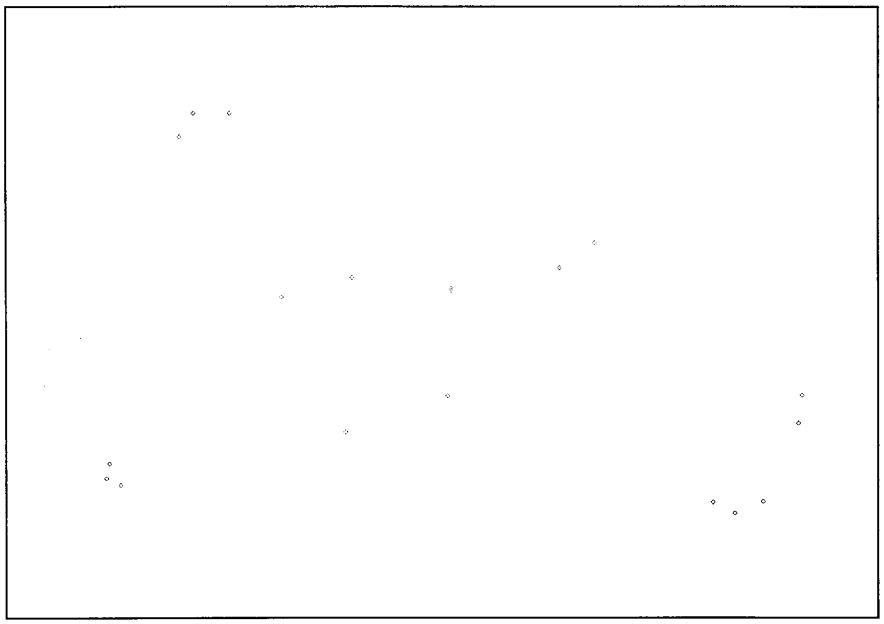


Fig. 10.106 Lucanidae

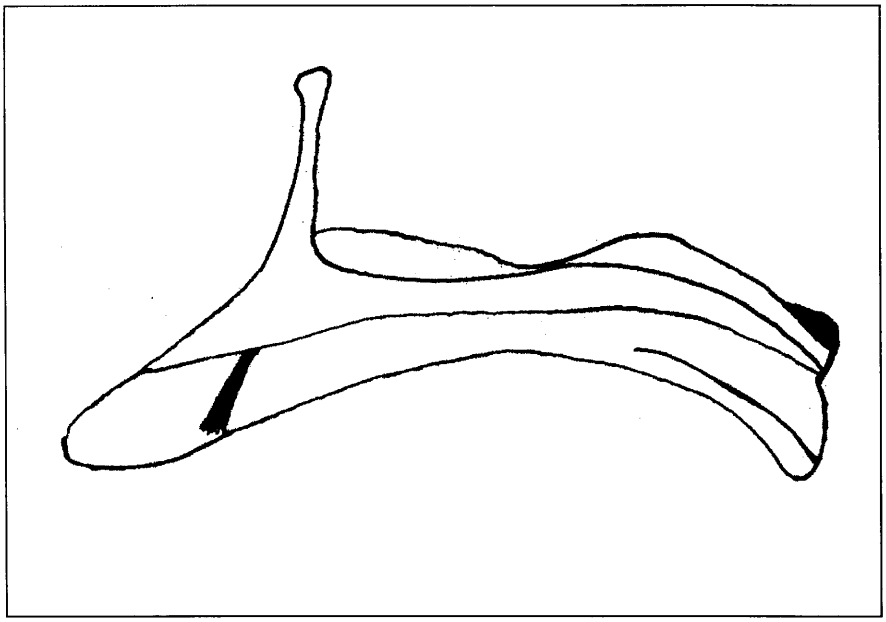


Fig. 10.107 Diphyllostomatidae

Fig. 10.106 Consensus configuration of landmarks of all studied species of Lucanidae; **Fig. 10.107** Consensus configuration of landmarks of all studied species of Diphyllostomatidae.

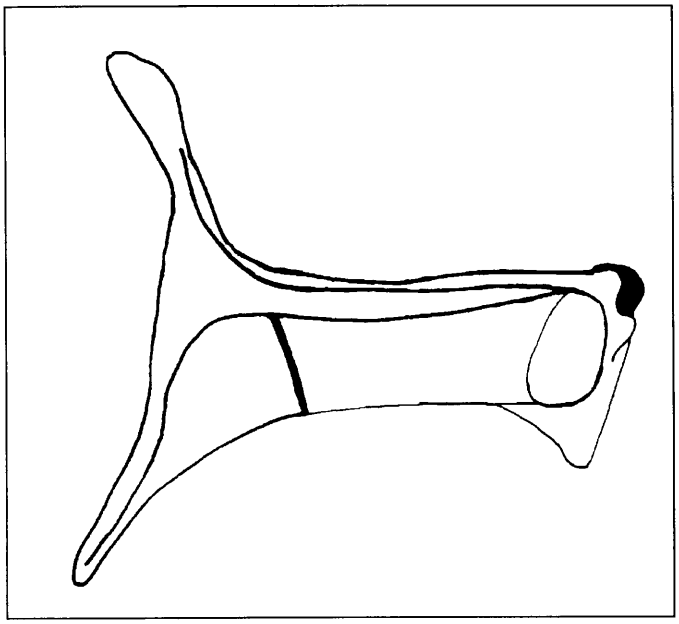


Fig. 10.108 Glaphyridae

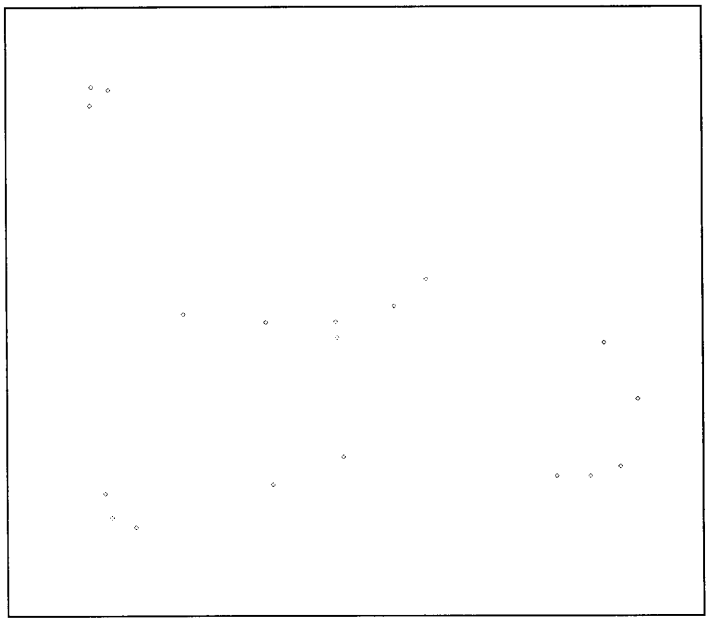


Fig. 10.109 Trogidae

Fig. 10.108 Consensus configuration of landmarks of all studied species of Glaphyridae; **Fig. 10.109** Consensus configuration of landmarks of all studied species of Trogidae.

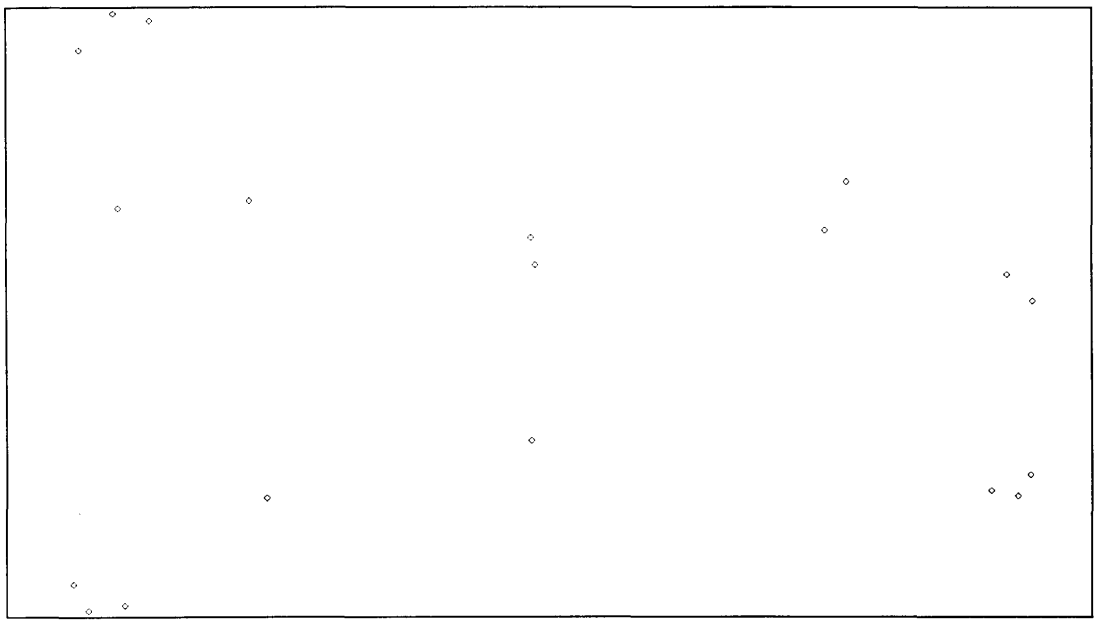


Fig. 10.110 Bolboceratidae

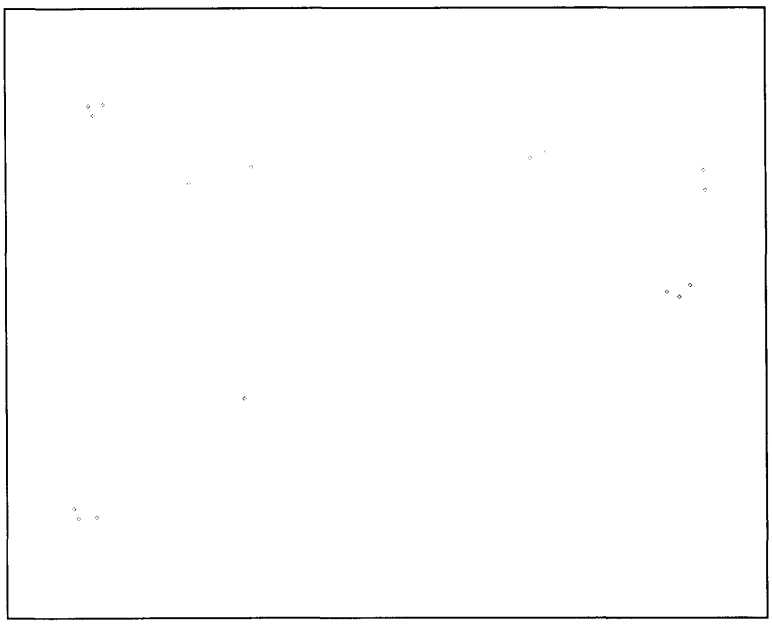


Fig. 10.111 Pleocomidae

Fig. 10.110 Consensus configuration of landmarks of all studied species of Bolboceratidae;

Fig. 10.111 Consensus configuration of landmarks of all studied species of Pleocomidae.

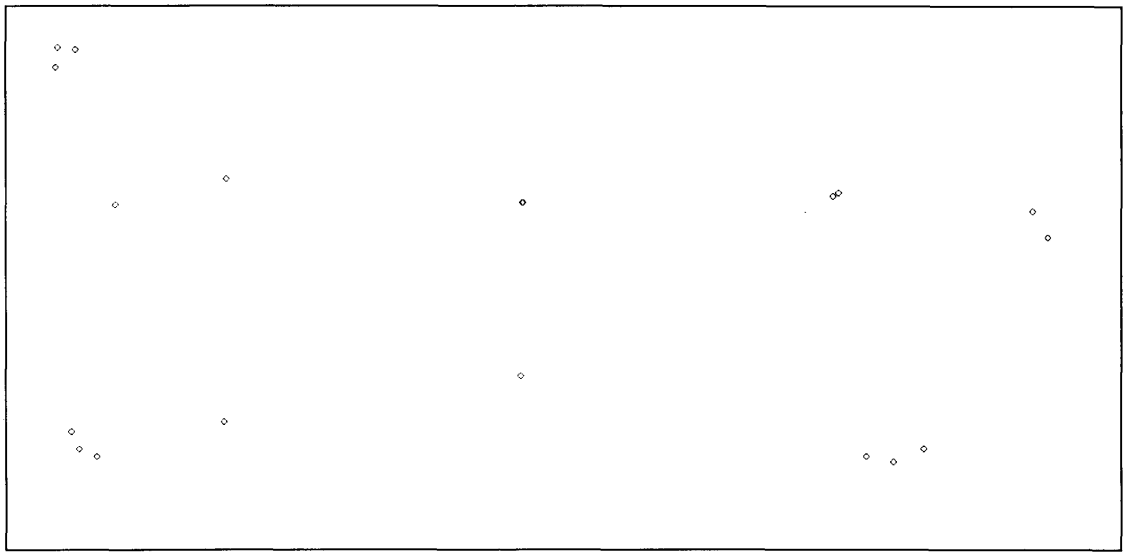


Fig. 10.112 Geotrupidae

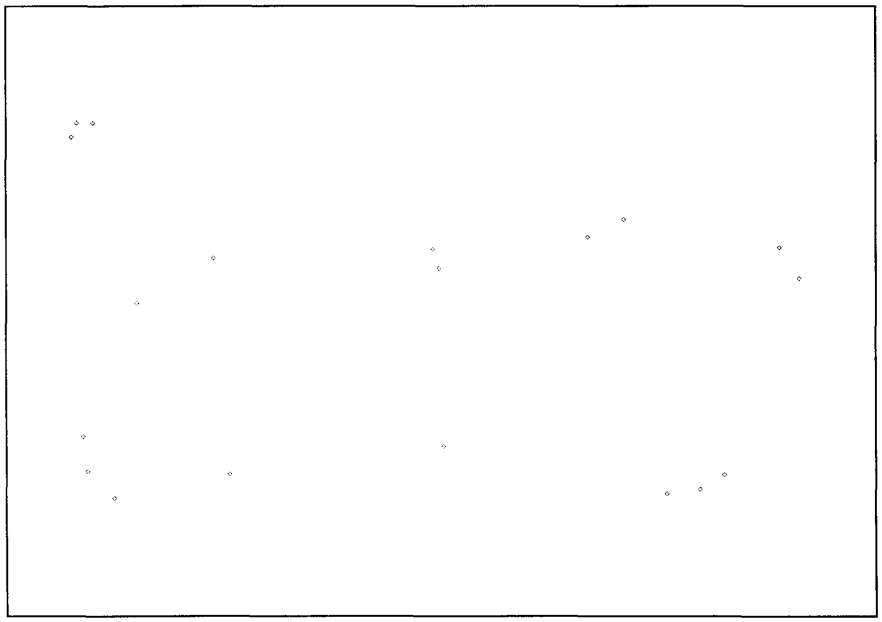


Fig. 10.113 Ochodaeidae

Fig. 10.112 Consensus configuration of landmarks of all studied species of Geotrupidae;
Fig. 10.113 Consensus configuration of landmarks of all studied species of Ochodaeidae.

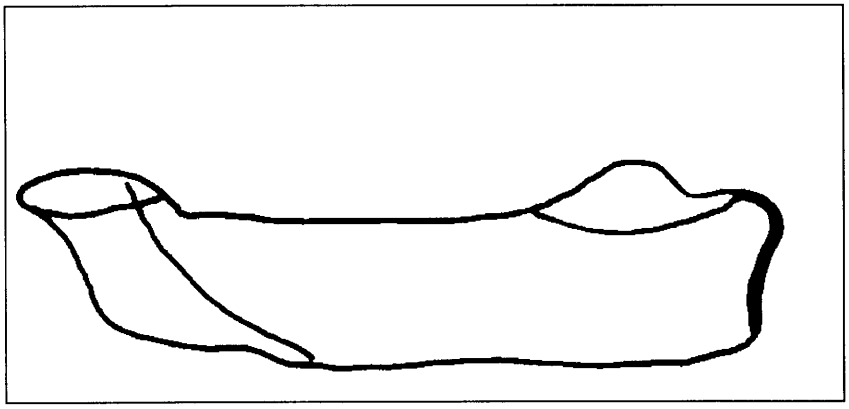


Fig. 10.114 Ceratocanthidae

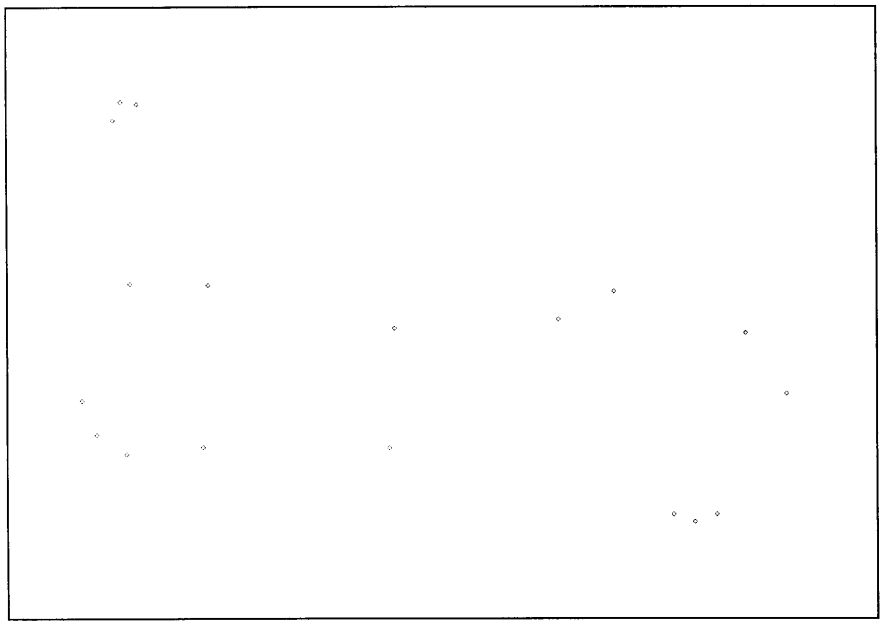


Fig. 10. 115 Hybosoridae

Fig.10.114 Consensus configuration of landmarks of all studied species of Ceratocanthidae;

Fig. 10.115 Consensus configuration of landmarks of all studied species of Hybosoridae.

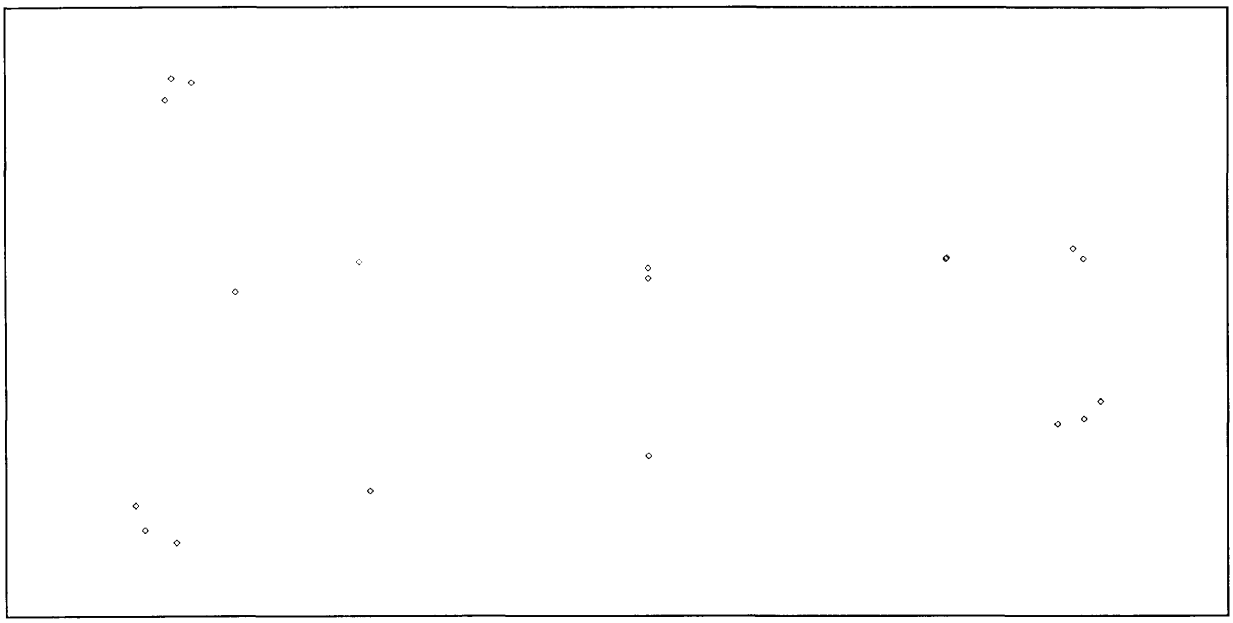


Fig. 10.116 Scarabaeidae: Aphodiinae

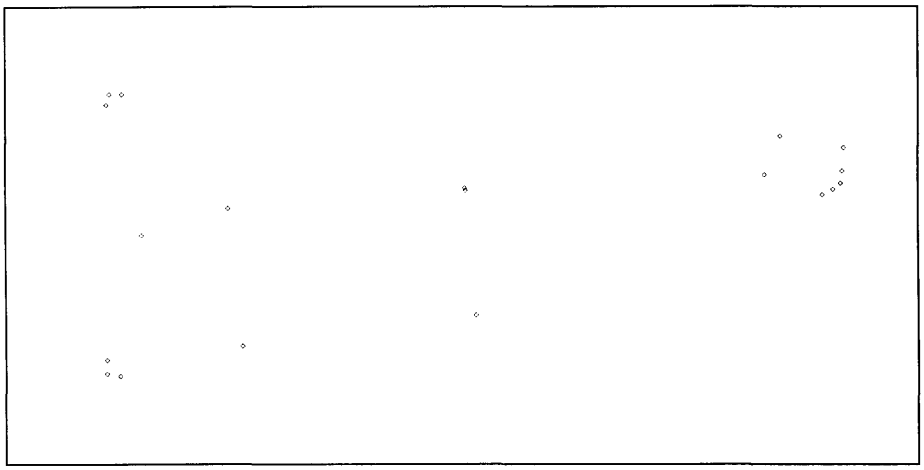


Fig. 10.117 Scarabaeidae: Scarabaeinae

Fig. 10.116 Consensus configuration of landmarks of all studied species of Aphodiinae (Scarabaeidae); **Fig. 10.117** Consensus configuration of landmarks of all studied species of Scarabaeinae (Scarabaeidae).

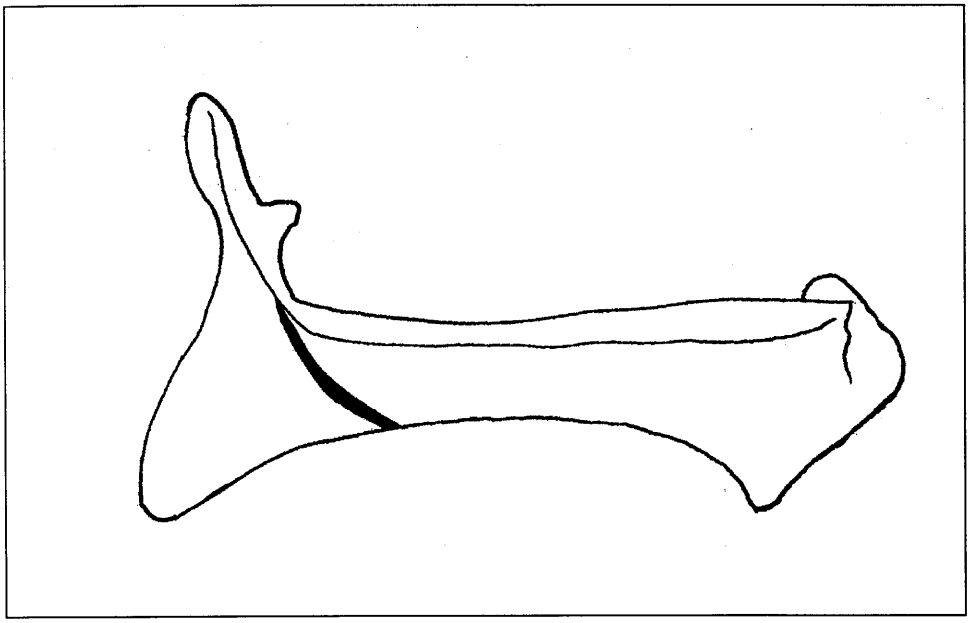


Fig. 10.118 Scarabaeidae: Orphninae

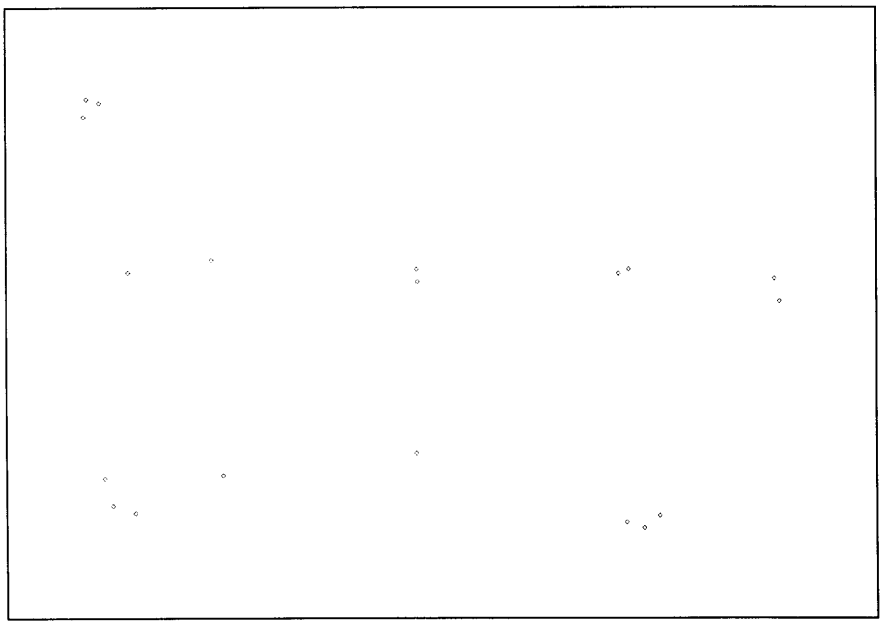


Fig. 10.119 Scarabaeidae: Melolonthinae

Fig. 10.118 Consensus configuration of landmarks of all studied species of Orphninae (Scarabaeidae); **Fig. 10.119** Consensus configuration of landmarks of all studied species of Melolonthinae (Scarabaeidae).

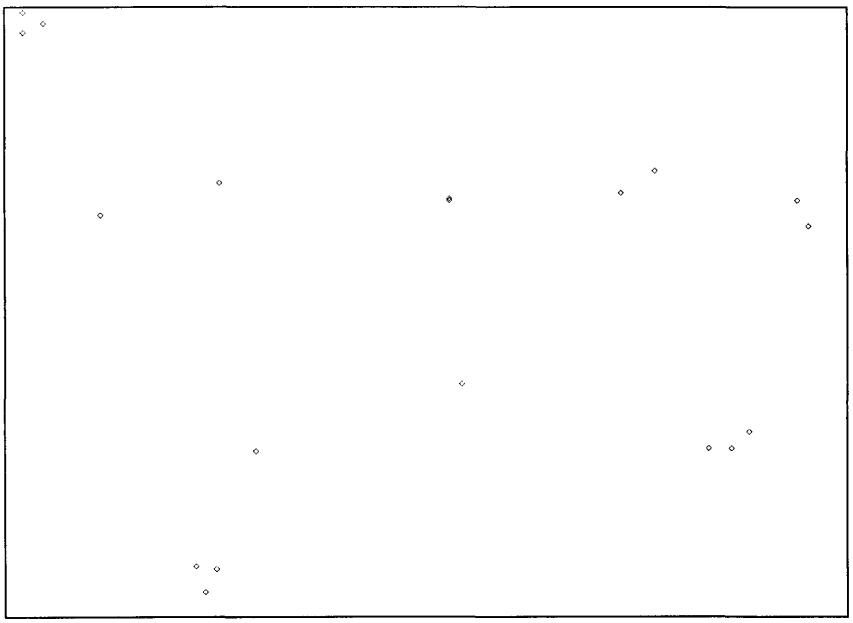


Fig. 10.120 Scarabaeidae: Hopliinae

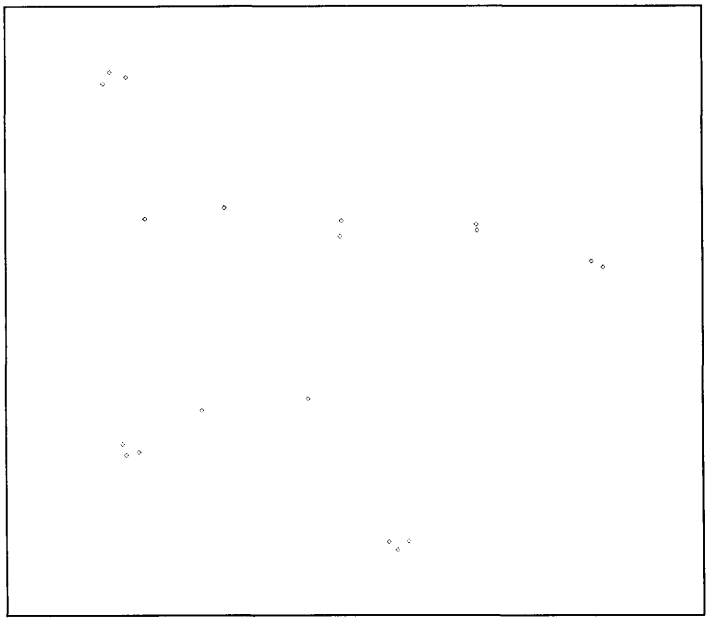


Fig. 10.121 Scarabaeidae: Rutelinae

Fig. 10. 120 Consensus configuration of landmarks of all studied species of Hopliinae (Scarabaeidae); **Fig. 10.121** Consensus configuration of landmarks of all studied species of Rutelinae (Scarabaeidae).

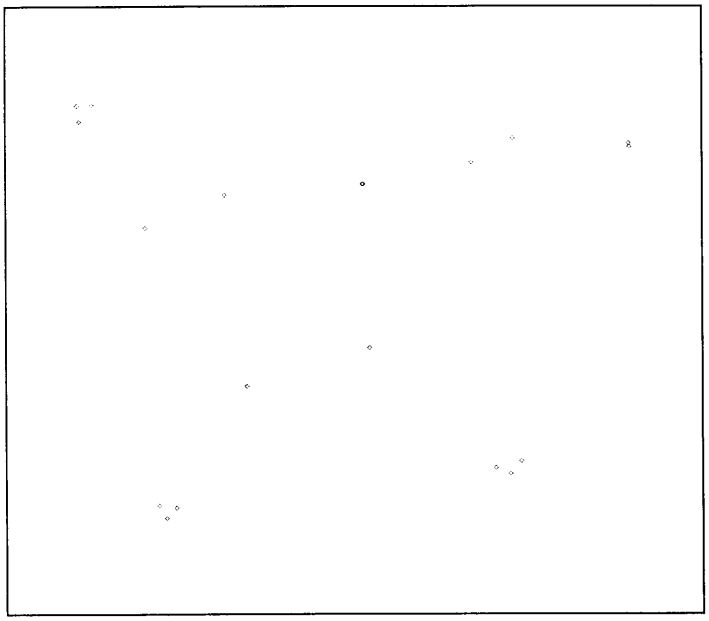


Fig. 10.122 Scarabaeidae: Dynastinae

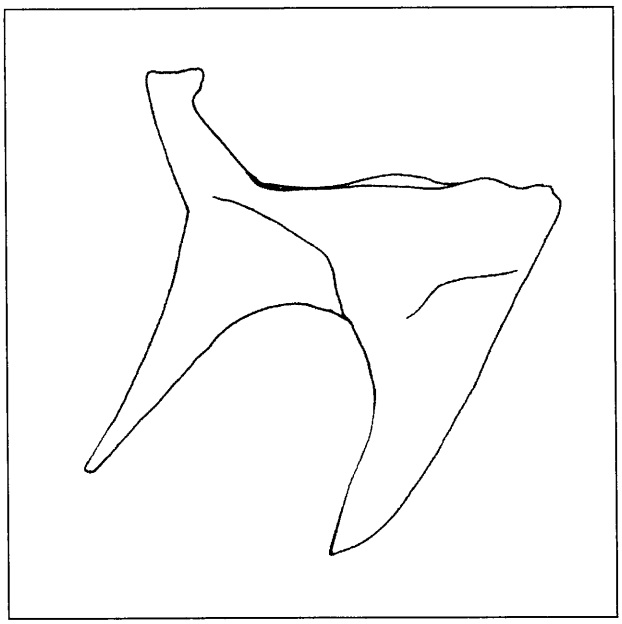


Fig. 10.123 Scarabaeidae: Trichiinae

Fig. 10.122 Consensus configuration of landmarks of all studied species of Dynastinae (Scarabaeidae); **Fig. 10.123** Consensus configuration of landmarks of all studied species of Trichiinae (Scarabaeidae).

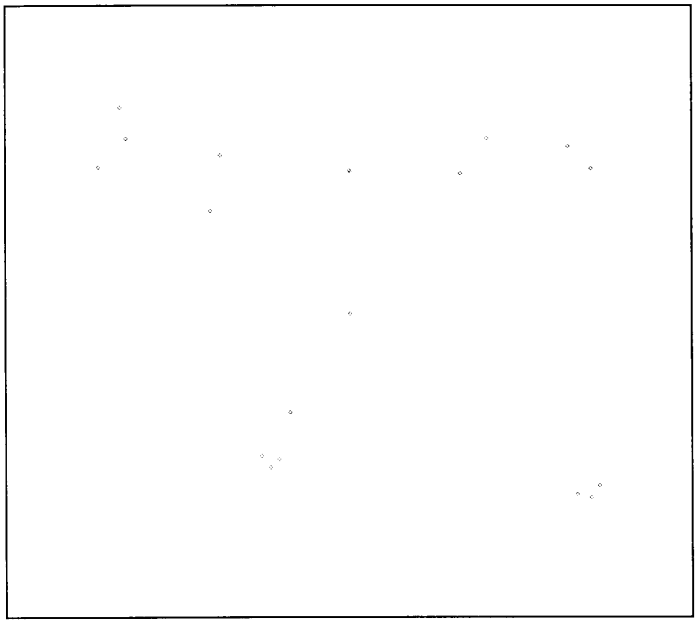


Fig 10.124 Scarabaeidae: Cetoniinae

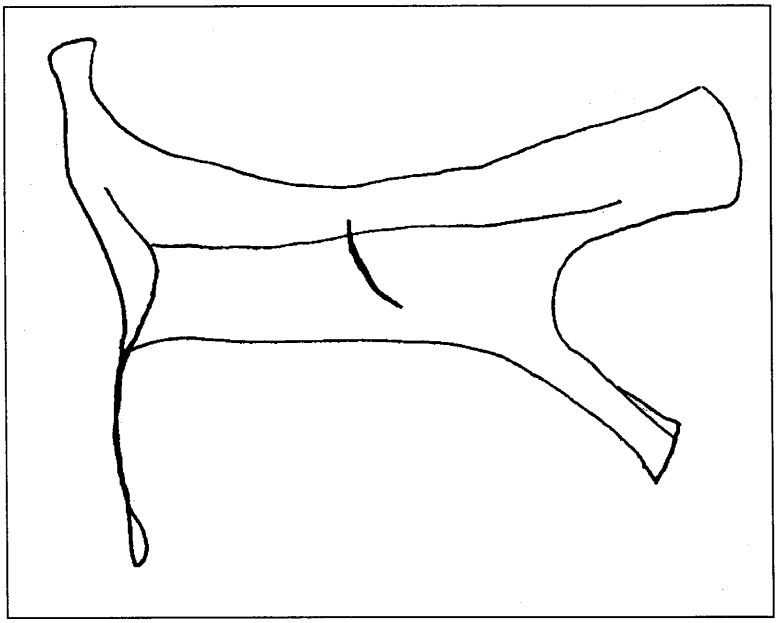


Fig. 10.125 Scarabaeidae: Valginae

Fig. 10.124 Consensus configuration of landmarks of all studied species of Cetoniinae (Scarabaeidae); **Fig. 10.125** Consensus configuration of landmarks of all studied species of Valgiinae (Scarabaeidae).

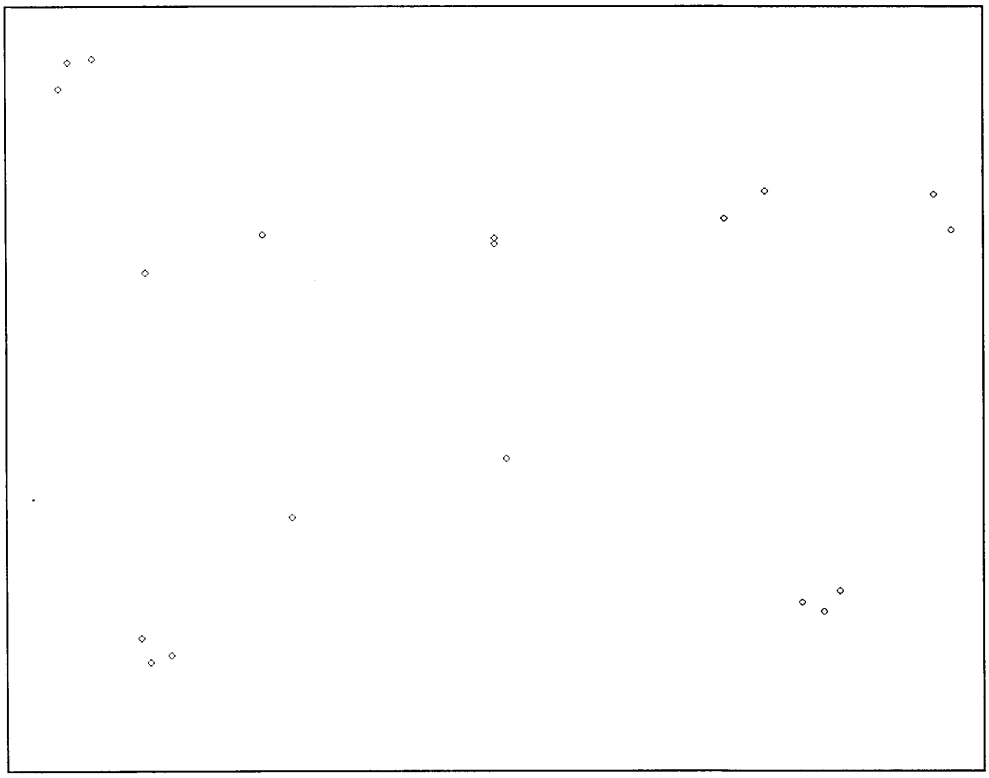


Fig. 10.126 Scarabaeidae

Fig. 10.126 Consensus configuration of landmarks of Scarabaeidae compiled from consensus configurations all subfamilies studied.

UNWARPED IMAGES OF EACH SPECIMEN WITHIN A TAXON

Unwarped images were computed only to acquire a general feeling for the data, and to determine the amount of morphological variation between the different species of each taxon. No statistical data are derived from unwarping images. Where a single species was used, no unwarped image could be derived as there was only one set of landmarks representing the consensus configuration of the taxon (these include Diphyllostomatidae, Glaphyridae, Ceratocanthidae, Orphninae (Scarabaeidae), Trichiinae (Scarabaeidae) and Valginae (Scarabaeidae)).

The pattern that emerged from the consensus configurations of the different taxa is more clearly visible in the unwarped images, where the different landmarks of individual species are plotted onto one another. Within species differences are clearly visible, but general trends within taxa are prominent. An example of this (the three different views of Trogidae and Cetoniinae) is given below (Fig 10.127 A, B, C and Fig. 10.128 A, B, C).

Fig. 10.127 A Unwarped images of frontal views of metendosternites of all studied Trogidae species.

Fig. 10.127 B Unwarped images of dorsal views of metendosternites of all studied Trogidae species.

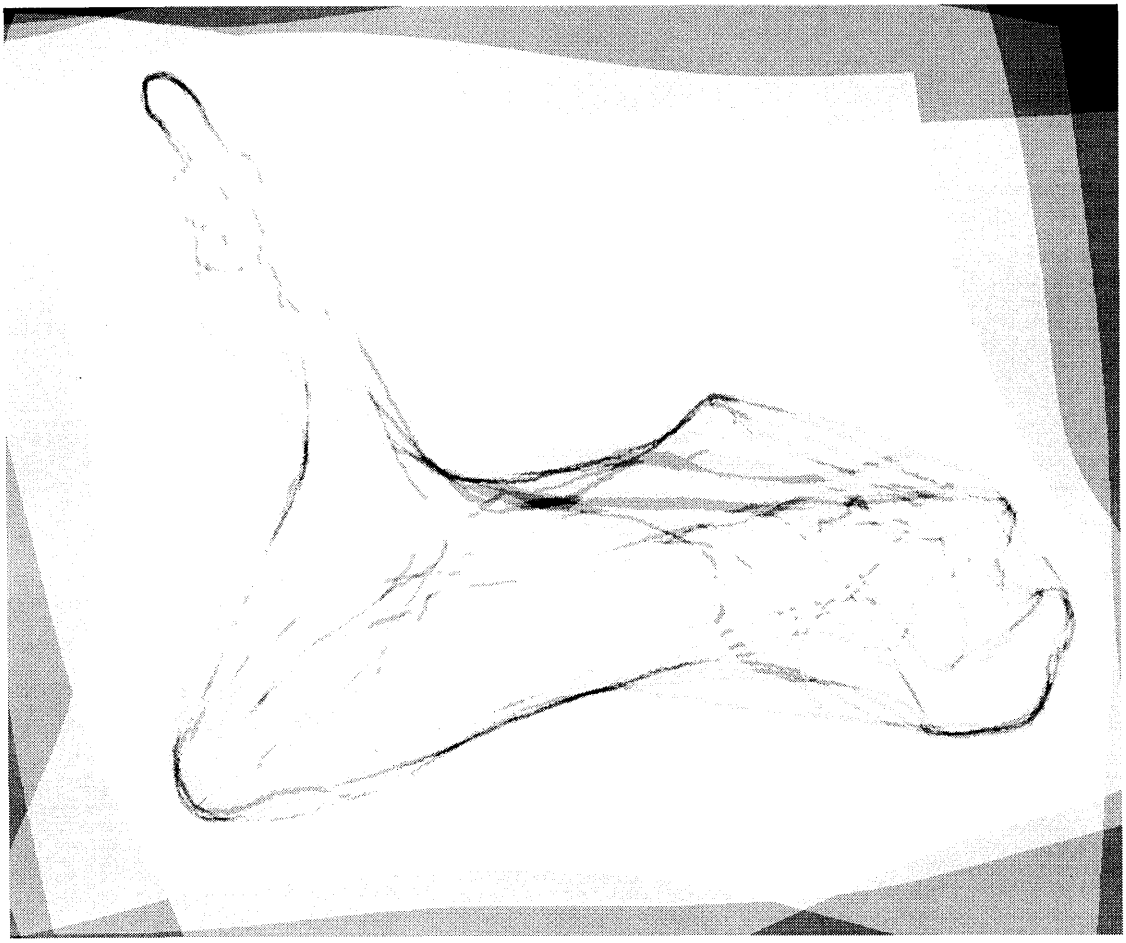


Fig. 10.127 C Unwarped images of lateral views of metendosternites of all studied Trogidae species.

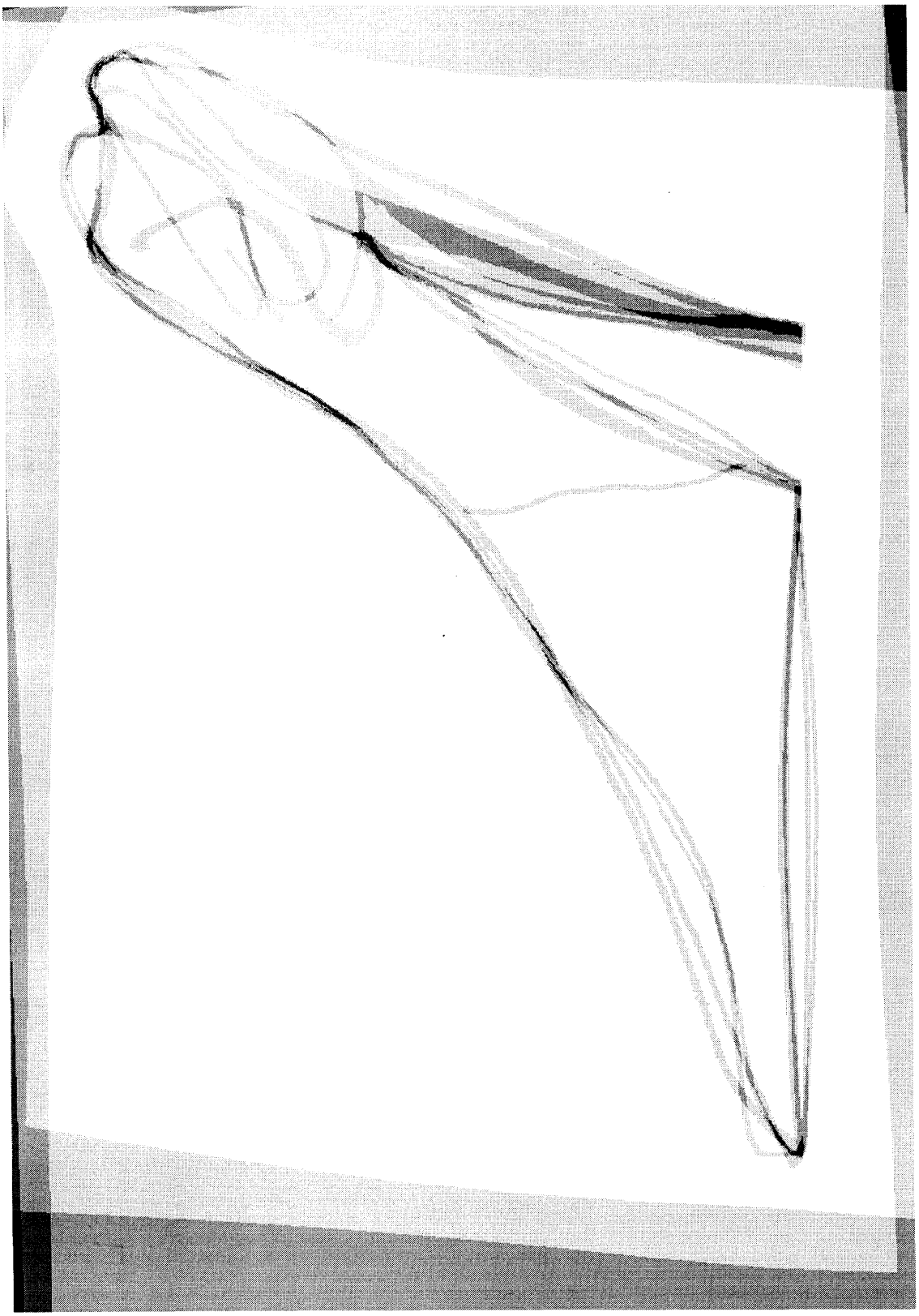


Fig. 10.127 A Unwarped images of frontal views of metendosternites of all studied Cetoniinae species.

Fig. 10.127 B Unwarped images of dorsal views of metendosternites of all studied Cetoniinae species.

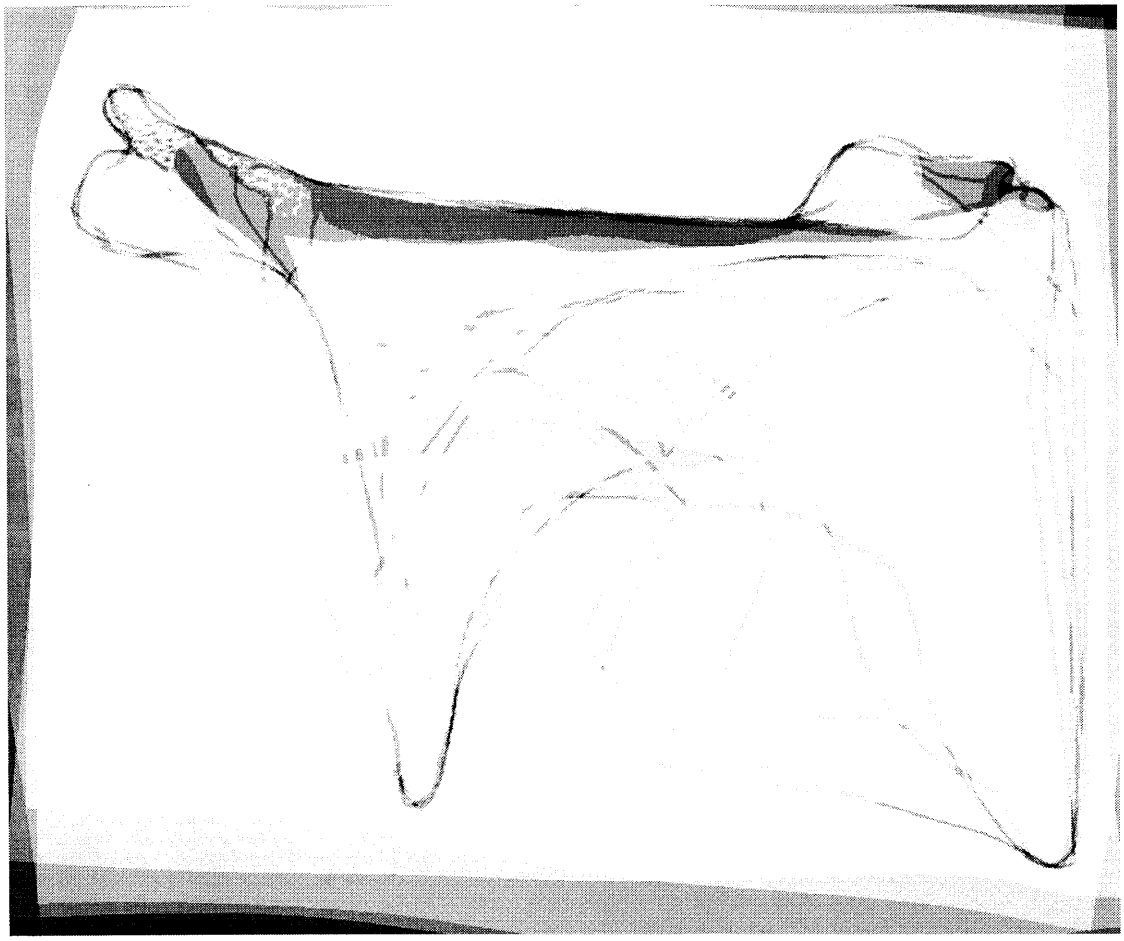


Fig. 10.127 C Unwarped images of lateral views of metendosternites of all studied Cetoniinae species.

ANALYSIS OF METENDOSTERNITES USING THIN-PLATE SPLINES

As mentioned previously, Glaresidae is the ancestor of the superfamily. In order to visually determine the correlation between Glaresidae and the rest of the taxa, Cartesian grids of the three views for each consensus configuration of the different taxa as deformations of Glaresidae are given in figures 10.129 to 10.195. The more primitive the taxon, the less deformed the Cartesian grid (this is a general pattern that can be detected in all three views).

Cartesian grids of primitive members of the Scarabaeoidea seem to show less deformation if compared to Glaresidae while landmark positions of members of Scarabaeoidea show more differences compared to Glaresidae. Within the Scarabaeidae, the Cartesian grid for the Aphodiinae (the most primitive members of the taxon) compared to that of Glaresidae shows the least deformation, while the Cartesian grid of Valginae (one of the most derived members of the Scarabaeoidea) compared to that of Glaresidae, shows the most deformation.

RESULTS (THIN-PLATE SPLINES) FROM THE FRONTAL VIEW

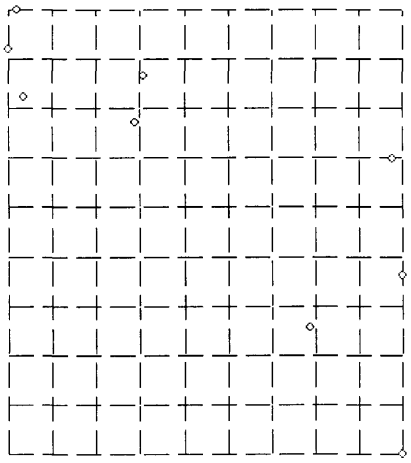


Fig. 10.129 Glaresidae

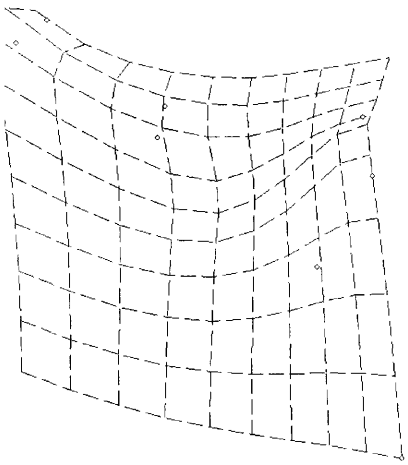


Fig. 10.130 Lucanidae

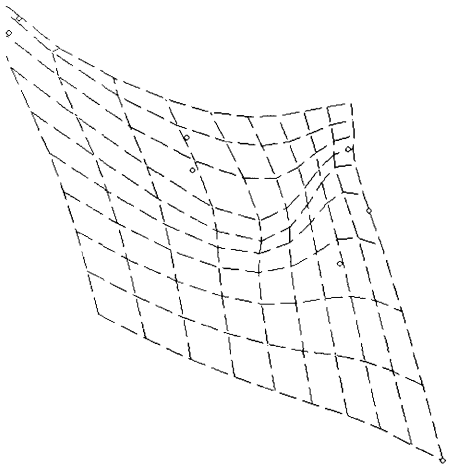


Fig 10.131 Diphylostomatidae

Fig. 10.129 Landmark configuration of Glaresidae; Cartesian grids of consensus configurations of different taxa as relative deformations of Glaresidae **Fig. 10.130** Lucanidae; **Fig. 10.131** Diphyllostomatidae

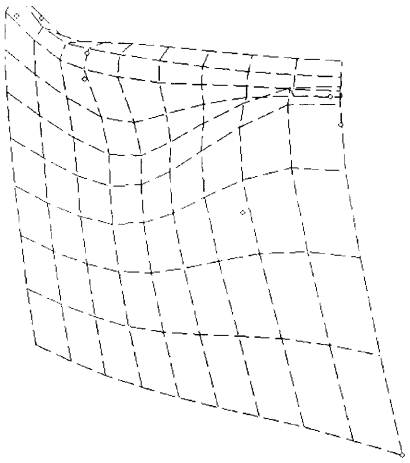


Fig. 10.132 Glaphyridae

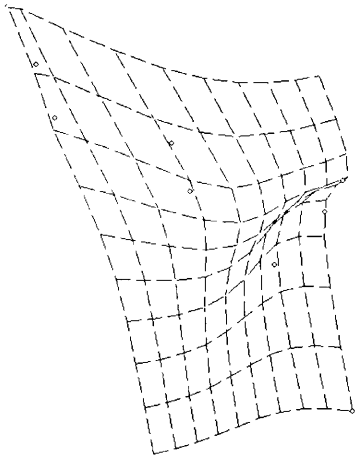


Fig. 10.133 Trogidae

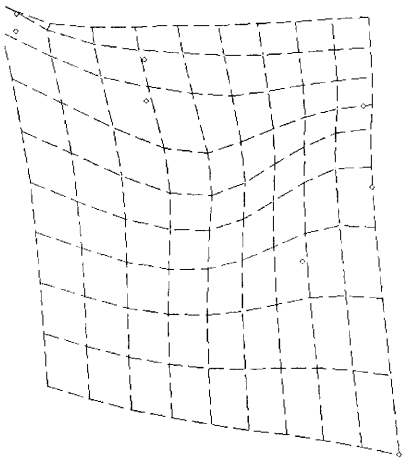


Fig. 10.134 Bolboceratidae

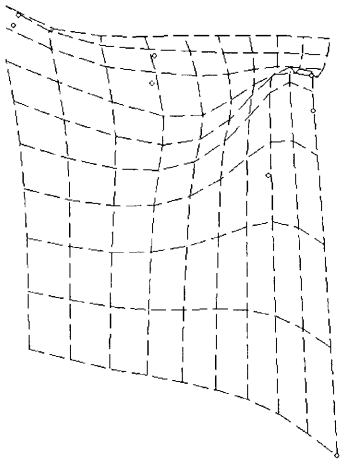


Fig. 10.135 Pleocomidae

Cartesian grids of consensus configurations of different taxa as relative deformations of Glaresidae **Fig. 10.132** Glaphyridae; **Fig. 10.133** Trogidae; **Fig. 10.134** Bolboceratidae; **Fig. 10.135** Pleocomidae.

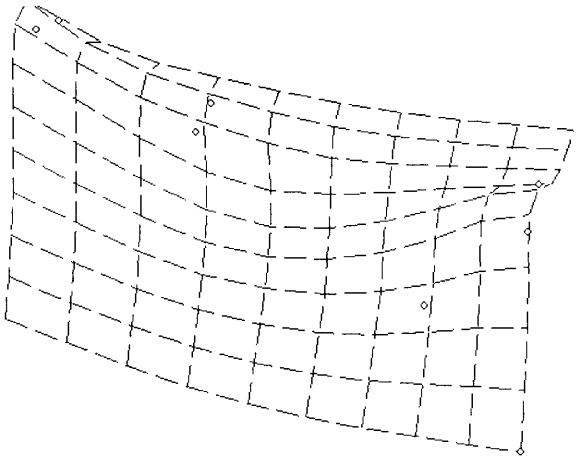


Fig. 10.136 Geotrupidae

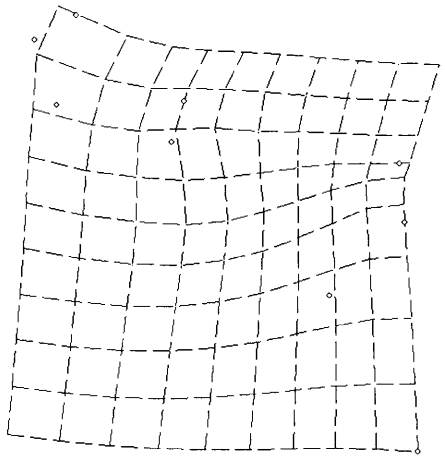


Fig. 10.137 Ochodaeidae

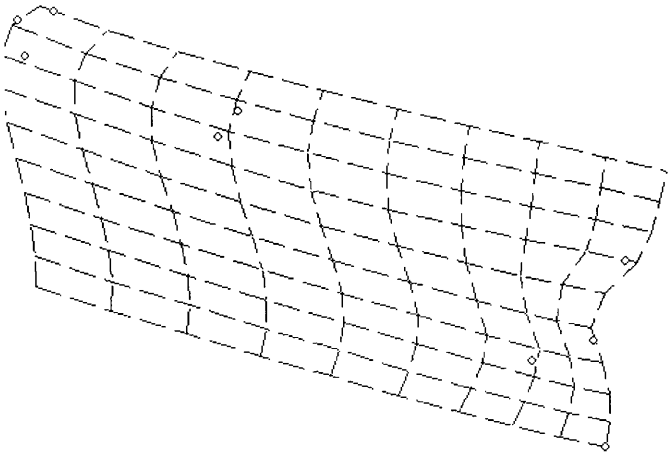


Fig. 10.138 Ceratocanthidae

Cartesian grids of consensus configurations of different taxa as relative deformations of Glaresidae **Fig. 10.136** Geotrupidae; **Fig. 10.137** Ochodaeidae; **Fig. 10.138** Ceratocanthidae.

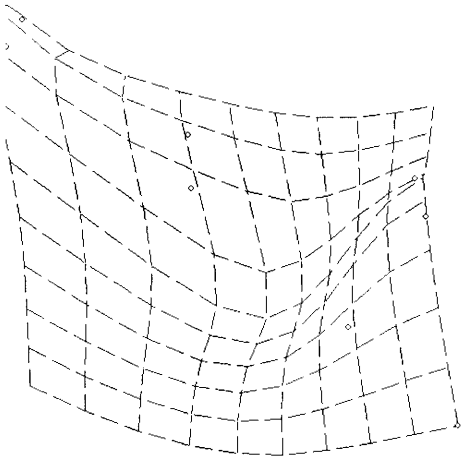


Fig. 10.139 Hybosoridae

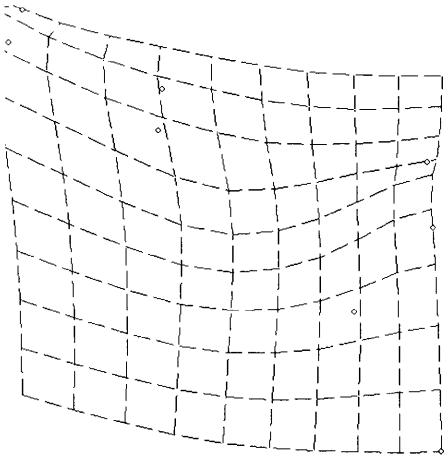


Fig. 10.140 Scarabaeidae: Aphodiinae

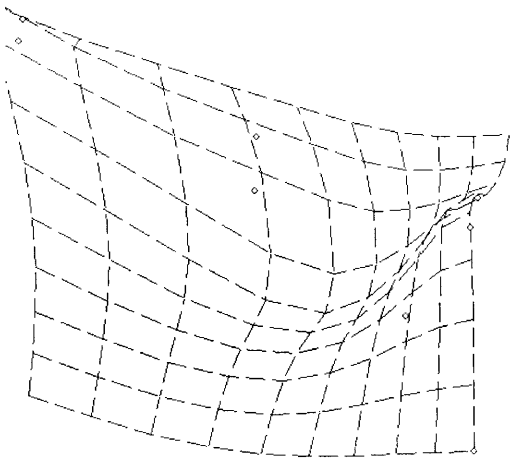


Fig. 10.141 Scarabaeidae: Scarabaeinae

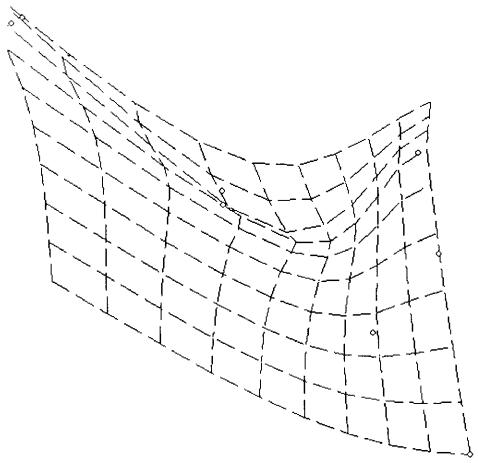


Fig. 10.142 Scarabaeidae: Orphninae

Cartesian grids of consensus configurations of different taxa as relative deformations of Glaresidae **Fig. 10.139** Hybosoridae; **Fig. 10. 140** Aphodiinae (Scarabaeidae); **Fig. 10.141** Scarabaeinae (Scarabaeidae); **Fig. 10.142** Orphninae (Scarabaeidae).

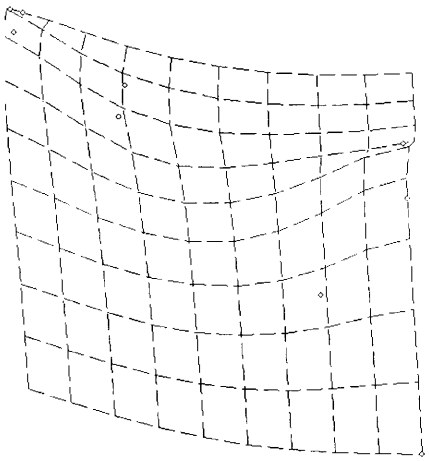


Fig. 10.143 Scarabaeidae: Melolonthinae

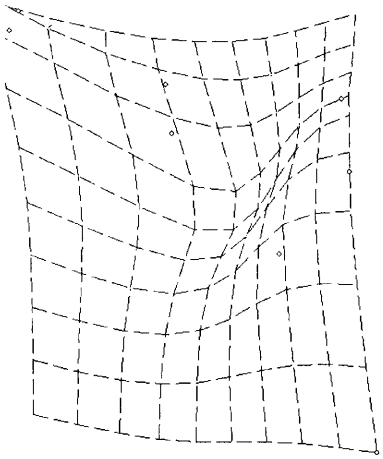


Fig 10.144 Scarabaeidae: Hopliinae

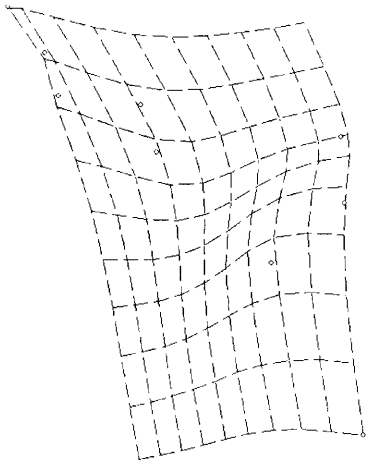


Fig. 10.145 Scarabaeidae: Rutelinae

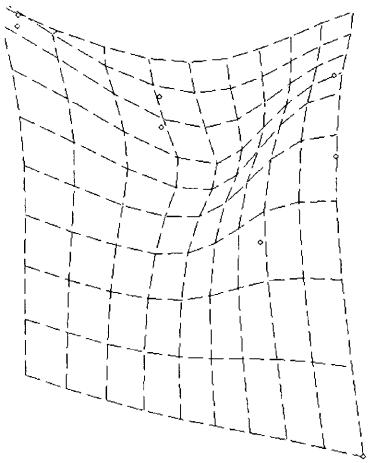


Fig. 10.146 Scarabaeidae: Dynastinae

Cartesian grids of consensus configurations of different taxa as relative deformations of Glaresidae **Fig. 10.143** Melolonthinae (Scarabaeidae); **Fig. 10. 144** Hopliinae (Scarabaeidae); **Fig. 10.145** Rutelinae (Scarabaeidae); **Fig. 10.146** Dynastinae (Scarabaeidae).

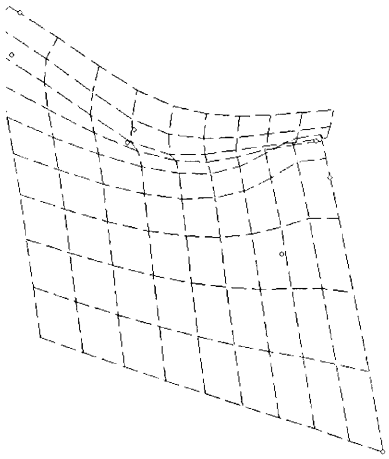


Fig. 10.147 Scarabaeidae: Trichiinae

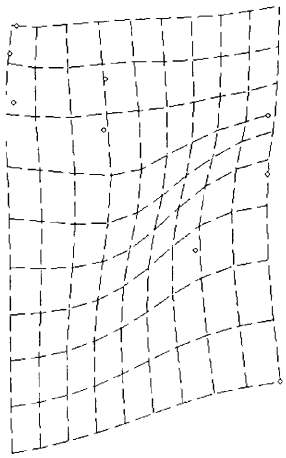


Fig. 10.148 Scarabaeidae: Cetoniinae

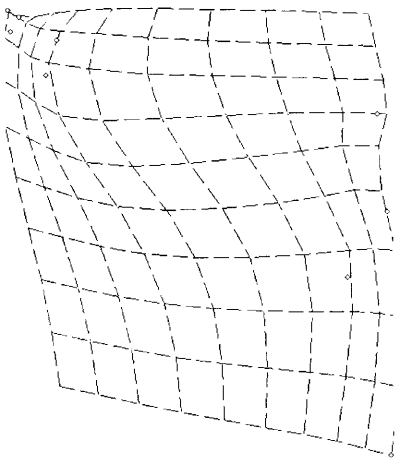


Fig. 10.149 Scarabaeidae: Valginae

Cartesian grids of consensus configurations of different taxa as relative deformations of Glaresidae **Fig. 10.147** Trichiinae (Scarabaeidae); **Fig. 10.148** Cetoniinae (Scarabaeidae); **Fig. 10.149** Valginae (Scarabaeidae).

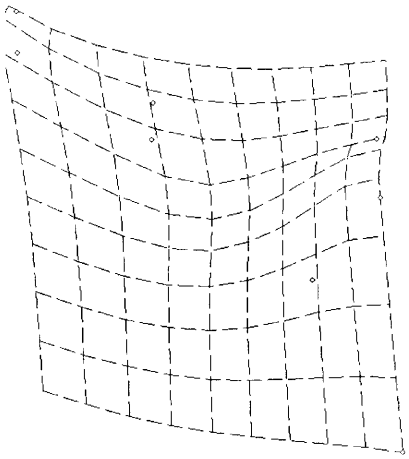


Fig. 10.150: Scarabaeidae

Fig. 10.150 Cartesian grid of consensus configuration of Scarabaeidae as deformation of Glaresidae.

RESULTS FROM THE DORSAL VIEWS

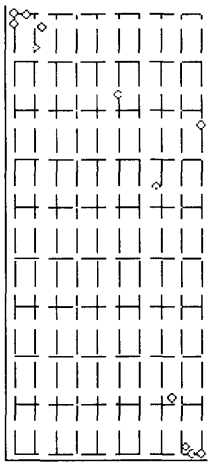


Fig. 10.151 Glaresidae

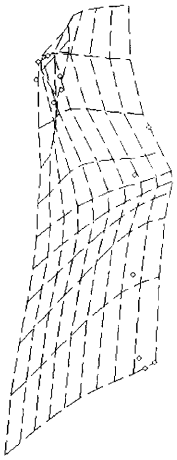


Fig. 10.152 Lucanidae

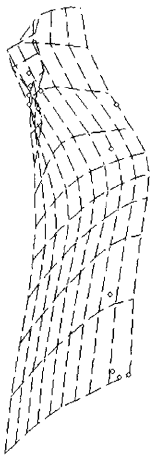


Fig. 10.153 Diphyllostomatidae

Fig. 10.151 Landmark configuration of Glaresidae; Cartesian grids of consensus configurations of different taxa as relative deformations of Glaresidae **Fig. 10.152** Lucanidae; **Fig. 10.153** Diphyllostomatidae.

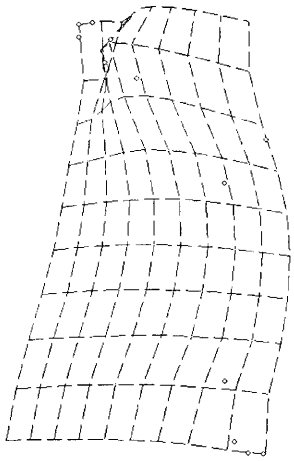


Fig. 10.154 Glaphyridae

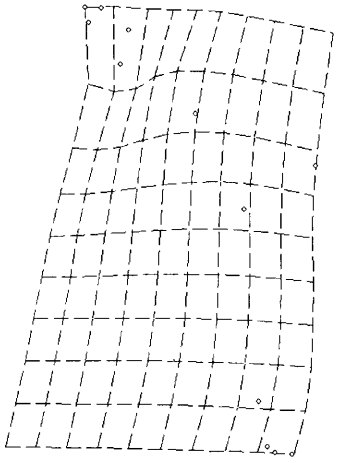


Fig. 10.155 Trogidae

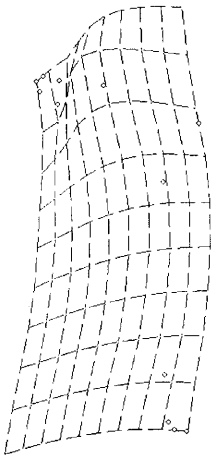


Fig. 10.156 Bolboceratidae

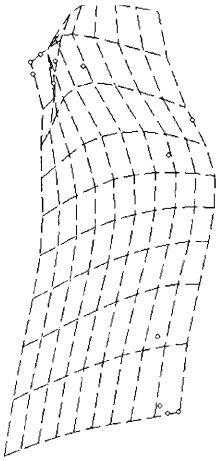


Fig. 10.157 Pleocomidae

Cartesian grids of consensus configurations of different taxa as relative deformations of Glaresidae **Fig. 10.154** Glaphyridae; **Fig. 10.155** Trogidae; **Fig. 10.156** Bolboceratidae; **Fig. 10.157** Pleocomidae.

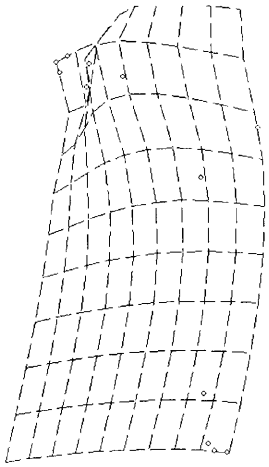


Fig. 10.158 Geotrupidae

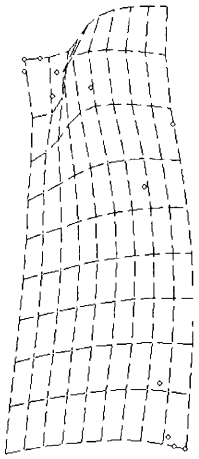


Fig. 10.159 Ochodaeidae

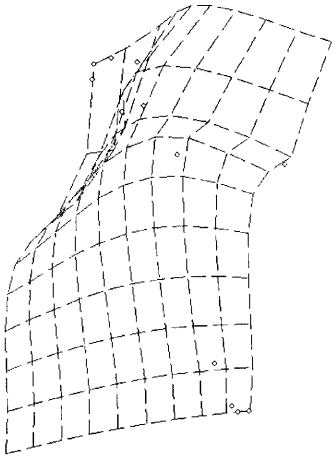


Fig. 10.160 Ceratocanthidae

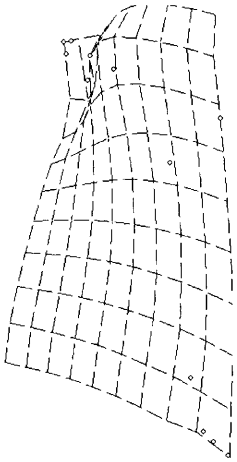


Fig. 10.161 Hybosoridae

Cartesian grids of consensus configurations of different taxa as relative deformations of Glaresidae **Fig. 10.158** Geotrupidae; **Fig. 10.159** Ochodaeidae; **Fig. 10.160** Ceratocanthidae; **Fig. 10.161** Hybosoridae.

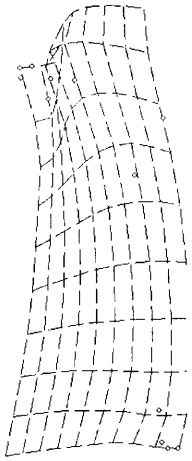


Fig. 10.162 Scarabaeidae: Aphodiinae

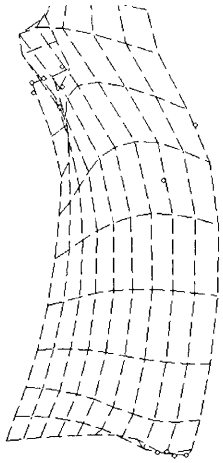


Fig. 10.163 Scarabaeidae: Scarabaeinae

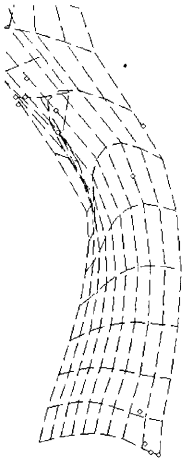


Fig. 10.164 Scarabaeidae: Orphninae

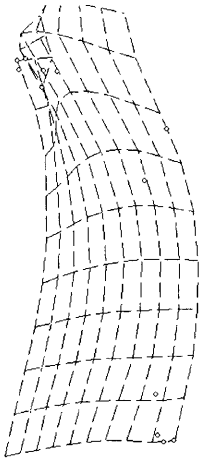


Fig. 10.165 Scarabaeidae: Melolonthinae

Cartesian grids of consensus configurations of different taxa as relative deformations of Glaresidae **Fig. 10.162** Aphodiinae (Scarabaeidae); **Fig. 10.163** Scarabaeinae (Scarabaeidae); **Fig. 10.164** Orphninae (Scarabaeidae); **Fig. 10.164** Melolonthinae (Scarabaeidae).

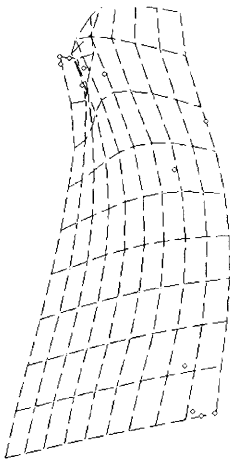


Fig. 10.167 Scarabaeidae: Hopliinae

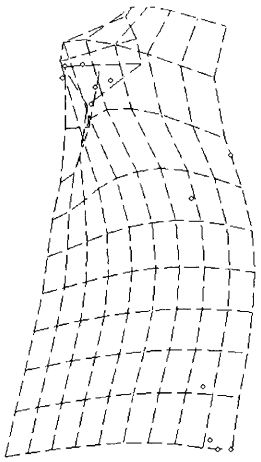


Fig. 10.168 Scarabaeidae: Rutelinae

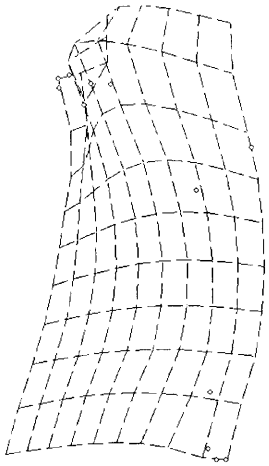
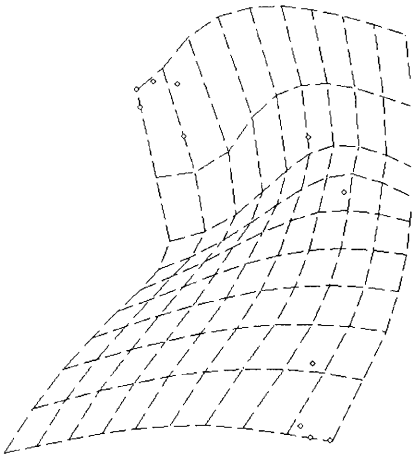


Fig. 10.169 Scarabaeidae: Dynastinae



Fig, 10.170 Scarabaeidae: Trichiinae

Cartesian grids of consensus configurations of different taxa as relative deformations of Glaresidae **Fig. 10.167** Hopliinae (Scarabaeidae); **Fig. 10.168** Rutelinae (Scarabaeidae); **Fig. 10.169** Dynastinae (Scarabaeidae); **Fig. 10.170** Trichiinae (Scarabaeidae).

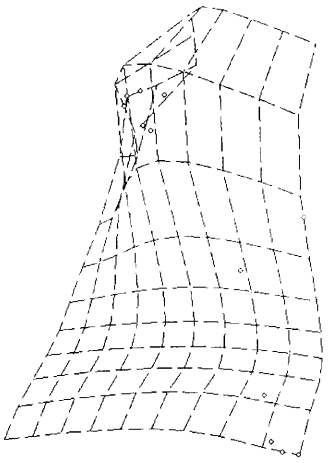


Fig. 10.171 Scarabaeidae: Cetoniinae

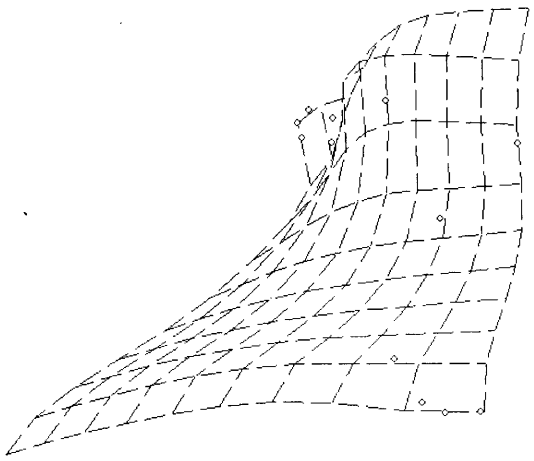


Fig. 10.172 Scarabaeidae: Valginae

Cartesian grids of consensus configurations of different taxa as relative deformations of Glaresidae **Fig. 10. 171** Cetoniinae (Scarabaeidae; **Fig. 10.17** Valginae (Scarabaeidae).

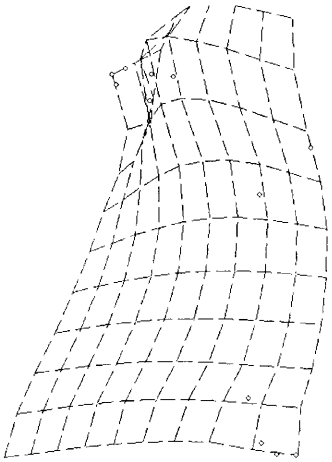


Fig. 10.173 Scarabaeidae

Fig. 10.173 Cartesian grid of consensus configuration of Scarabaeidae as deformation of Glaresidae.

RESULTS FROM THE LATERAL VIEWS

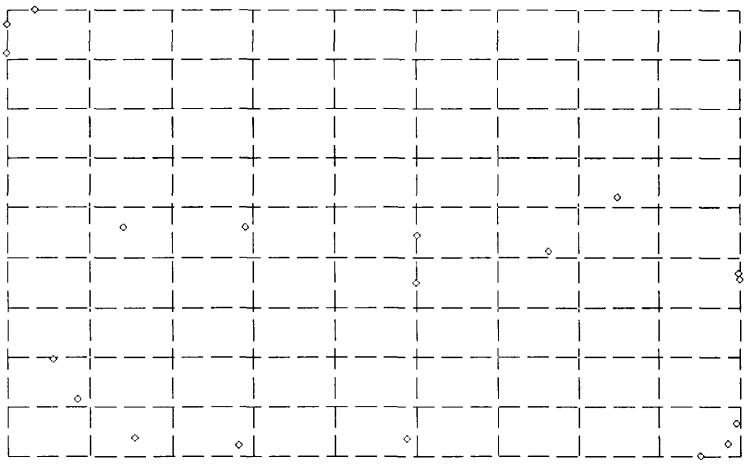


Fig. 10.174 Glaresidae

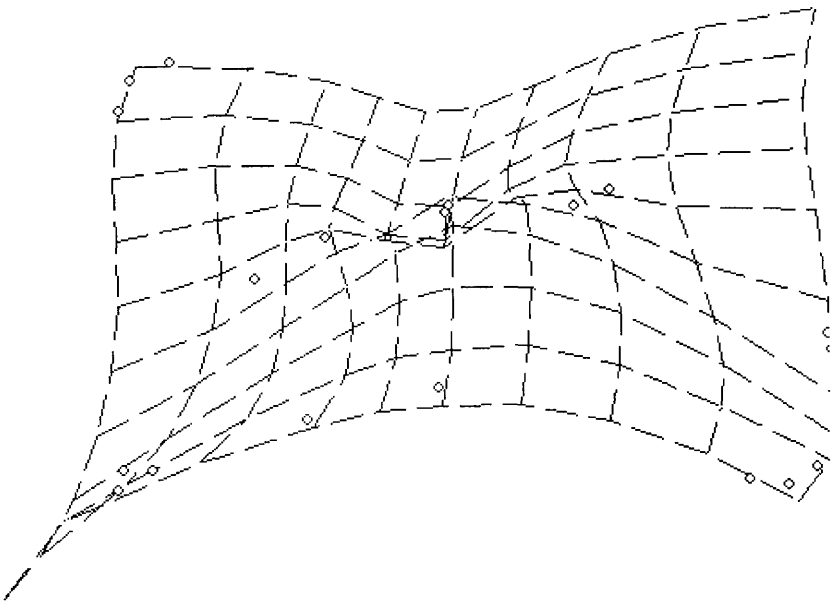


Fig. 10.175 Lucanidae

Fig. 10.174 Cartesian grid of Glaresidae; Cartesian grids of consensus configurations of different taxa as relative deformations of Glaresidae **Fig. 10.175** Lucanidae.

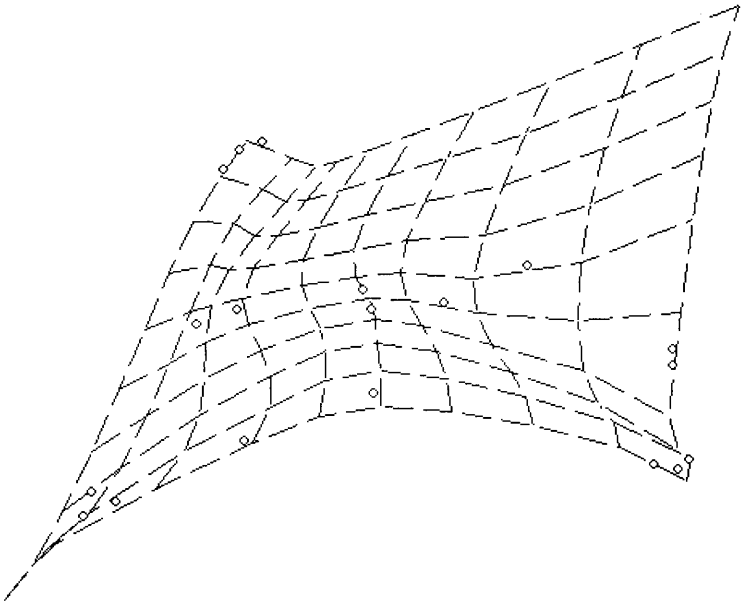


Fig. 10.176 Diphylostomatidae

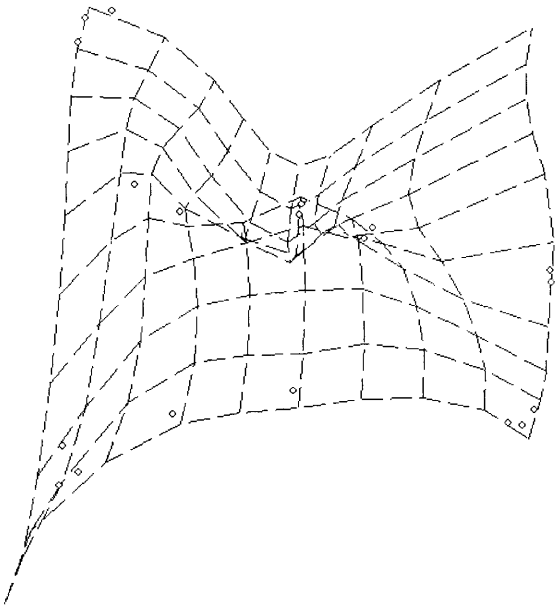


Fig. 10 177 Glaphyridae

Cartesian grids of consensus configurations of different taxa as relative deformations of Glaresidae **Fig. 10.176** Diphyllostomatidae; **Fig. 10.177** Glaphyridae.

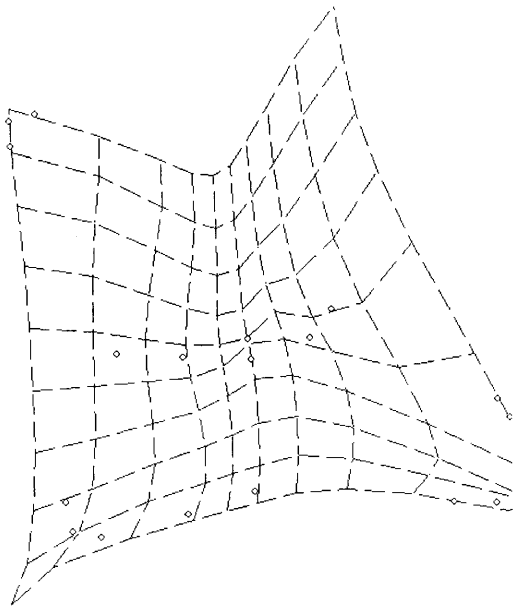


Fig. 10.178 Trogidae

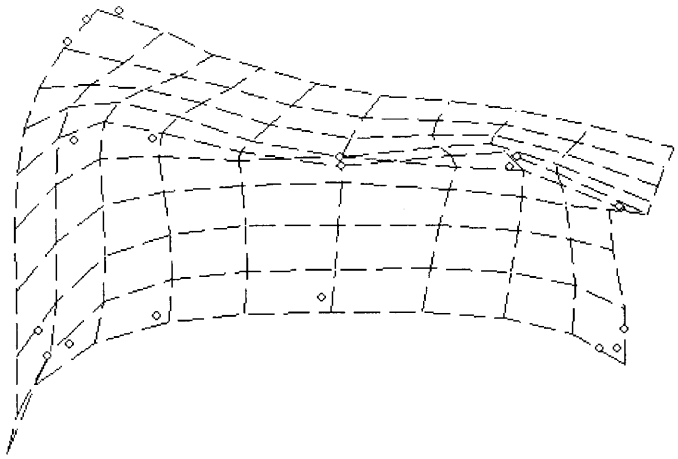


Fig. 10.179 Bolboceratidae

Cartesian grids of consensus configurations of different taxa as relative deformations of Glaresidae **Fig. 10.178** Trogidae; **Fig. 10.179** Bolboceratidae.

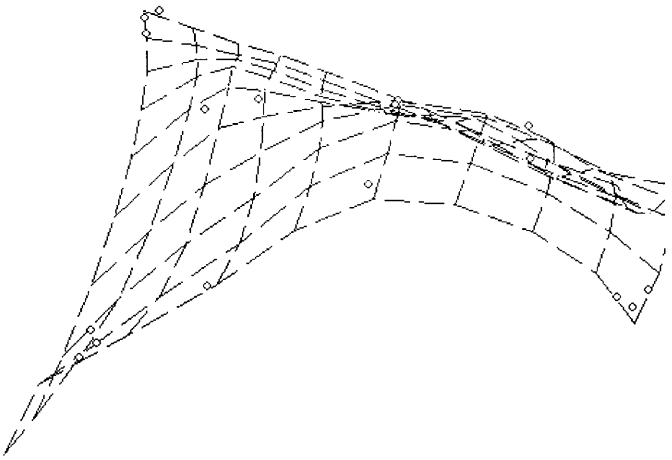


Fig. 10.180 Pleocomidae

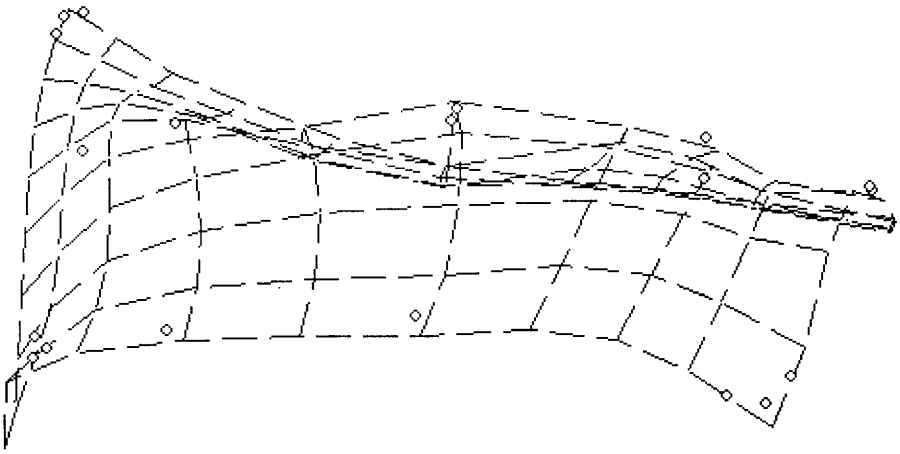


Fig. 10.181 Geotrupidae

Cartesian grids of consensus configurations of different taxa as relative deformations of Glaresidae **Fig. 10.180** Pleocomidae; **Fig. 10.181** Geotrupidae.

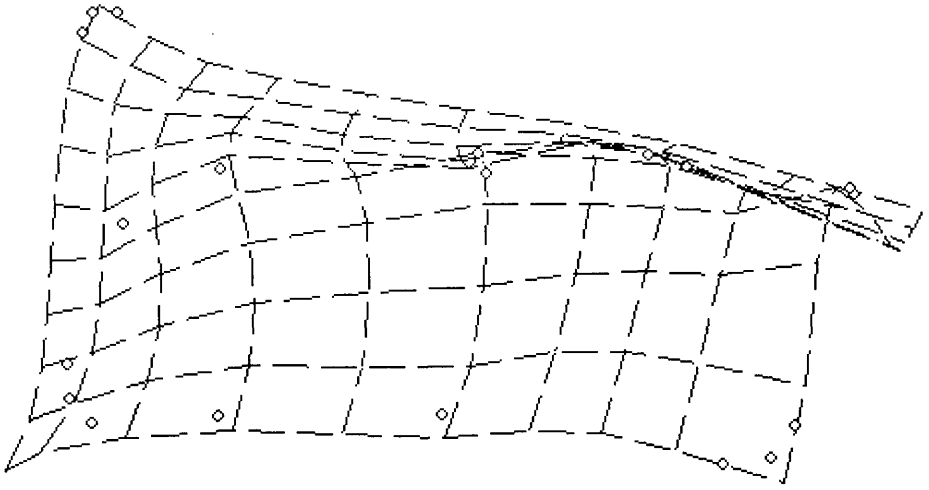


Fig. 10.182 Ochodaeidae

Fig. 10.183 Ceratocanthidae

Cartesian grids of consensus configurations of different taxa as relative deformations of Glaresidae **Fig. 10.182** Ochodaeidae; **Fig. 10.183** Ceratocanthidae.

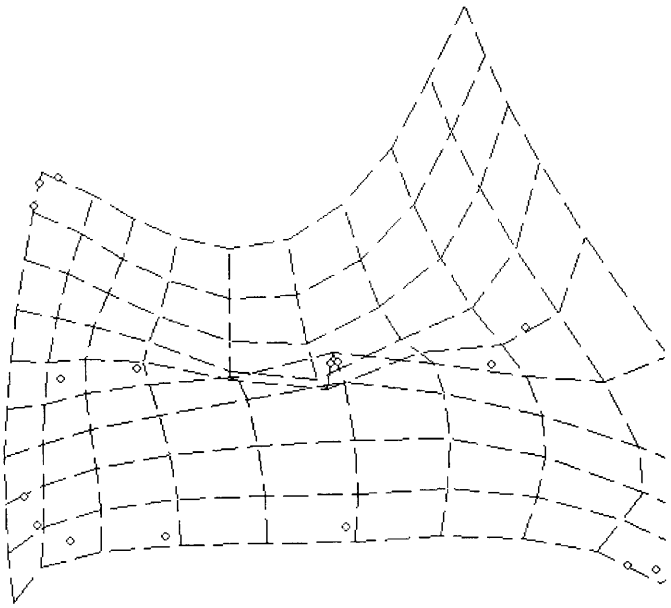


Fig. 10.184 Hybosoridae

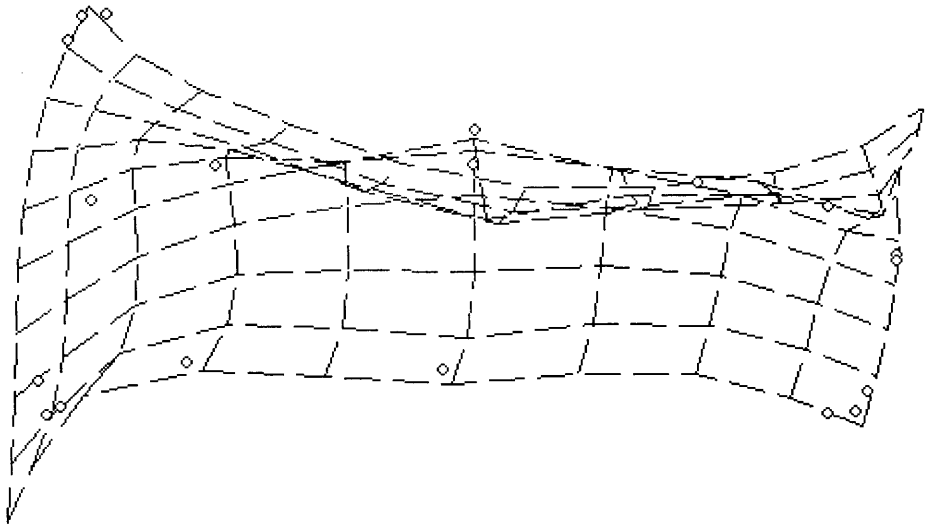


Fig. 10.185 Scarabaeidae: Aphodiinae

Cartesian grids of consensus configurations of different taxa as relative deformations of Glaresidae **Fig. 10.184** Hybosoridae; **Fig. 10.185** Aphodiinae (Scarabaeidae).

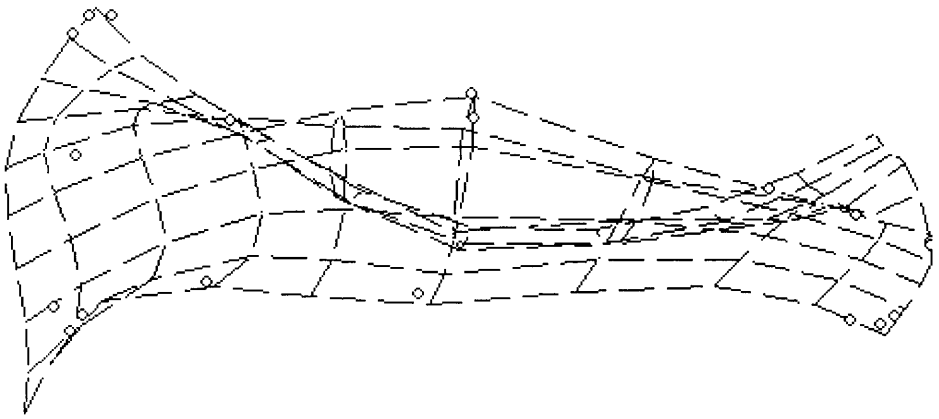


Fig. 10.186 Scarabaeidae: Scarabaeinae

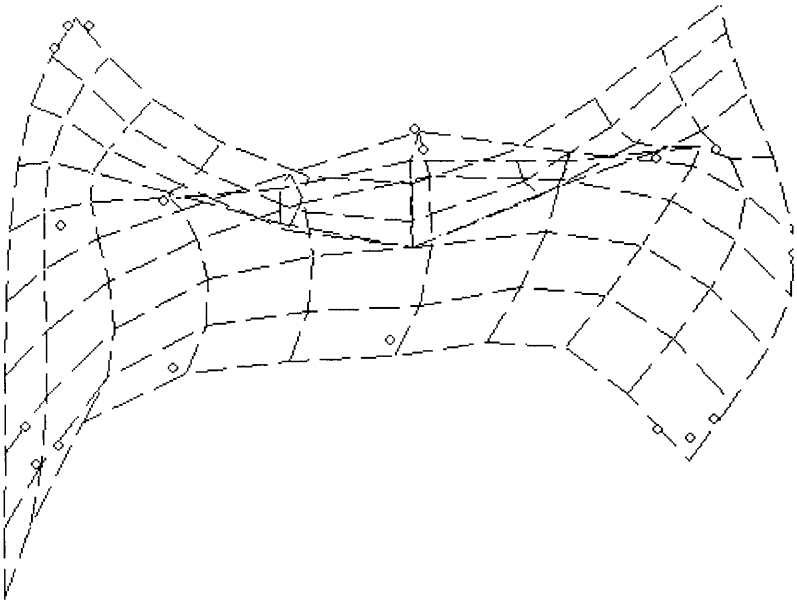


Fig. 10.187 Scarabaeidae: Orphninae

Cartesian grids of consensus configurations of different taxa as relative deformations of Glaresidae **Fig. 10.186** Scarabaeinae (Scarabaeidae); **Fig. 10.187** Orphninae (Scarabaeidae).

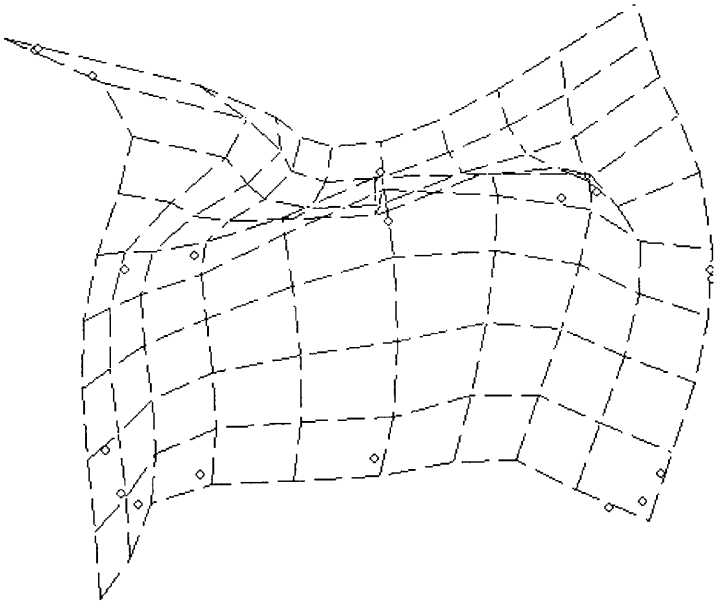


Fig. 10.188 Scarabaeidae: Melolonthinae

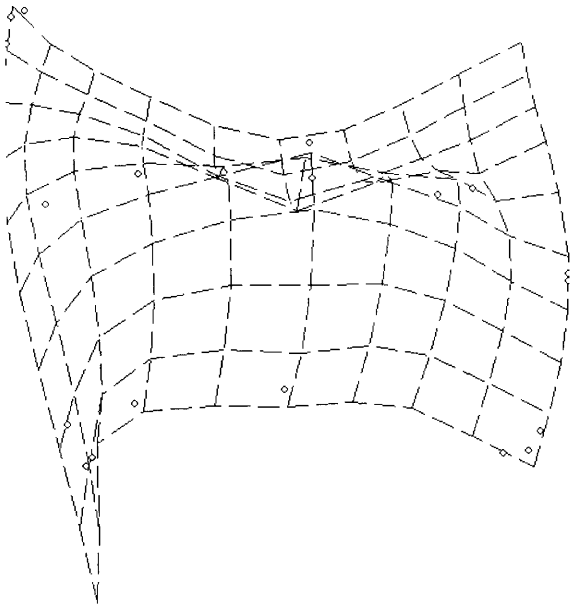


Fig. 10.189 Scarabaeidae: Hopliinae

Cartesian grids of consensus configurations of different taxa as relative deformations of Glaresidae **Fig. 10.188** Melolonthinae (Scarabaeidae); **Fig. 10.189** Hopliinae (Scarabaeidae).

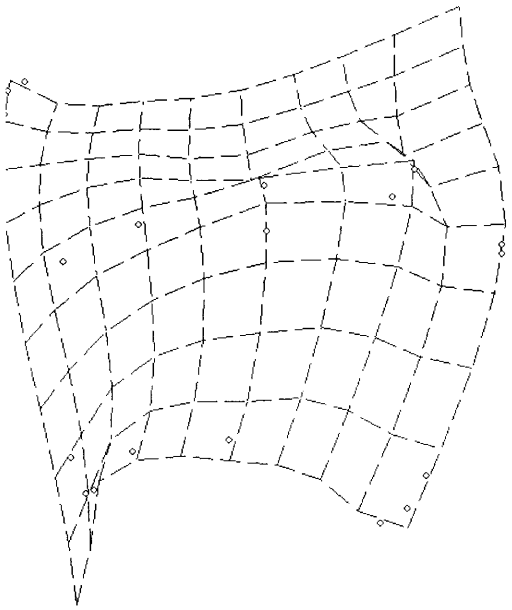


Fig. 10.190 Scarabaeidae: Rutelinae

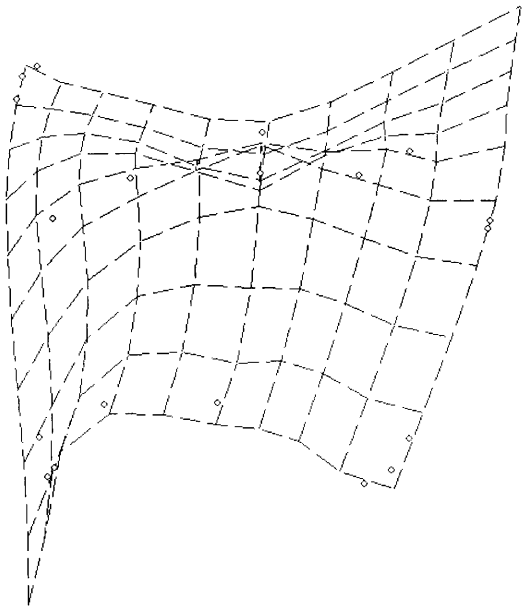


Fig. 10.191 Scarabaeidae: Dynastinae

Cartesian grids of consensus configurations of different taxa as relative deformations of Glaresidae **Fig. 10.190** Rutelinae (Scarabaeidae); **Fig. 10.191** Dynastinae (Scarabaeidae).

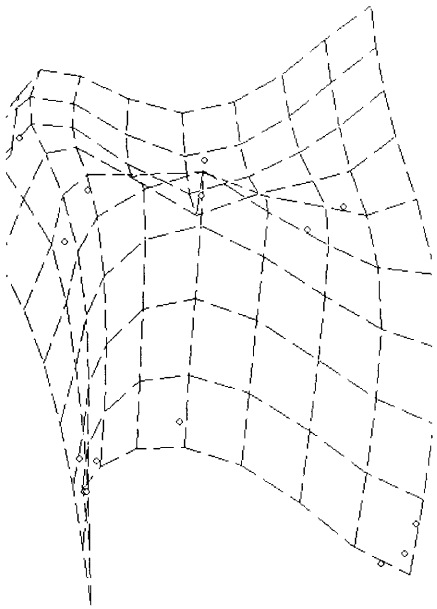


Fig. 10.192 Scarabaeidae: Trichiinae

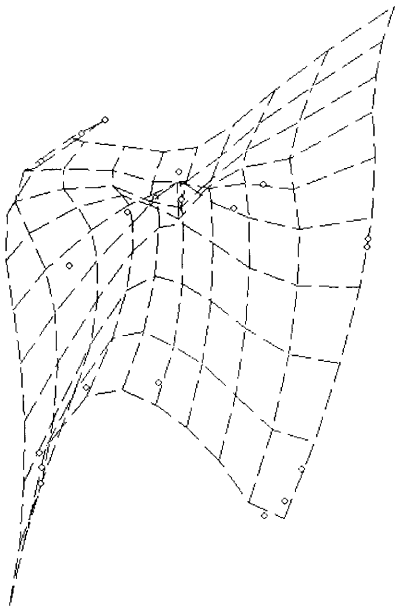


Fig. 10.193 Scarabaeidae: Cetoniinae

Cartesian grids of consensus configurations of different taxa as relative deformations of Glaresidae **Fig. 10.192** Trichiinae (Scarabaeidae); **Fig. 10.193** Cetoniinae (Scarabaeidae).

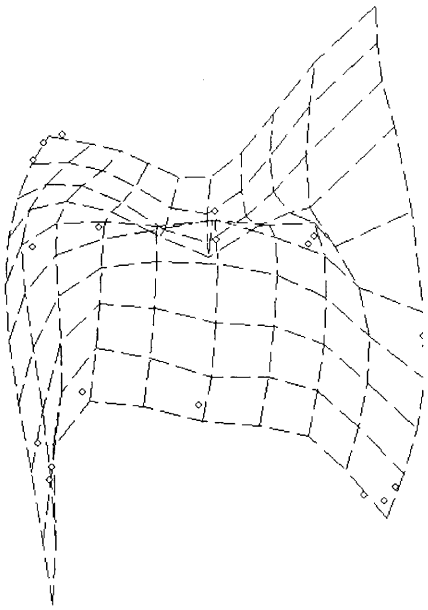


Fig. 10.194 Scarabaeidae: Valginae

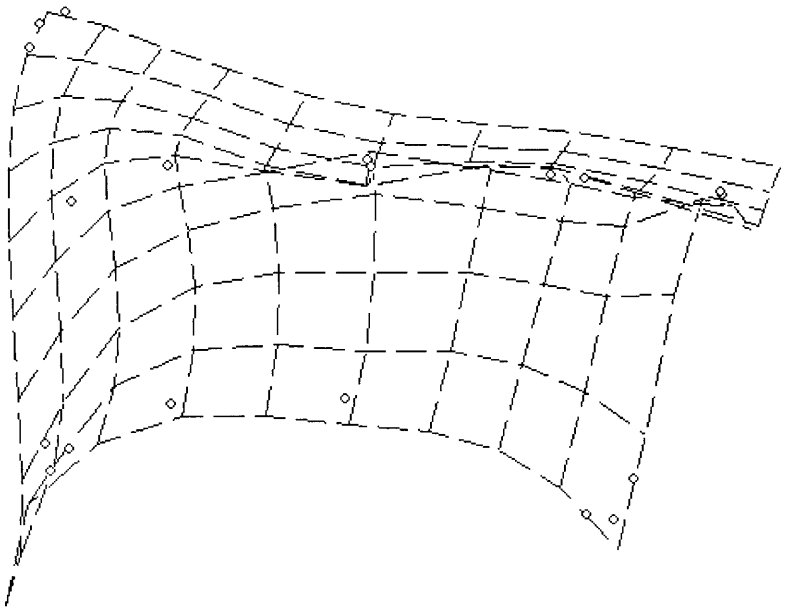


Fig. 10.195 Scarabaeidae

Fig. 10.194 Cartesian grid of consensus configuration of Valginae (Scarabaeidae) as deformation of Glaresidae and **Fig. 10.195** Cartesian grid of consensus configuration of all studied subfamilies of Scarabaeidae as deformation of Glaresidae.

CONSTRUCTION OF PHENETIC TREES TO DETERMINE PHENETIC RELATIONSHIPS BETWEEN THE FAMILIES

Triangular matrices of 55 Procrustes distances were computed for each view (three matrices for the three views of the Scarabaeidae and three matrices for the three views of the 12 families, including Scarabaeidae but excluding Passalidae). The six triangular matrices of Procrustes distances were subjected to UPGMA cluster analysis (unweighted pair-group method using arithmetic averages) using NTSYS-pc to generate phenetic trees to determine phenetic relationships between taxa. The UPGMA algorithm computes average similarity or dissimilarity of a taxon to an extant cluster weighting each taxon in that cluster equally regardless of its structural subdivision (Sneath & Sokal, 1973).

Phenetic trees of the 12 Scarabaeoidea families are presented in Figure 10.196 to Figure 10.198 and phenetic trees of the three views of the Scarabaeidae subfamilies are presented in figure 10.199 to Figure 10.201.

The vector distributions of the members of the "final" clusters of each phenogram (consisting of only two families) are plotted against one another to indicate the similarity of their landmark positions. The phenogram depicts the taxa within the "final" clusters as phenetically close to one another. In addition to this, the vector distributions of the landmark positions of Glaresidae are compared with that of Lucanidae and Diphyllostomatidae. Lucanidae and Diphyllostomatidae do not appear near Glaresidae on the phenograms, the reason being that their landmark positions in comparison to the Glaresidae, vary. These three families are, however, phylogenetically very close to one another and belong to the more primitive families within the Scarabaeoidea. They also appear close to one another on the cladogram produced by Browne & Scholtz (1995; in press). The phenogram depicts only positional and shape differences in the landmarks among the families and not ancestor/descendant relationships. (These three families are taken only as an example, the same comparisons can be made by using other families within the Scarabaeoidea).

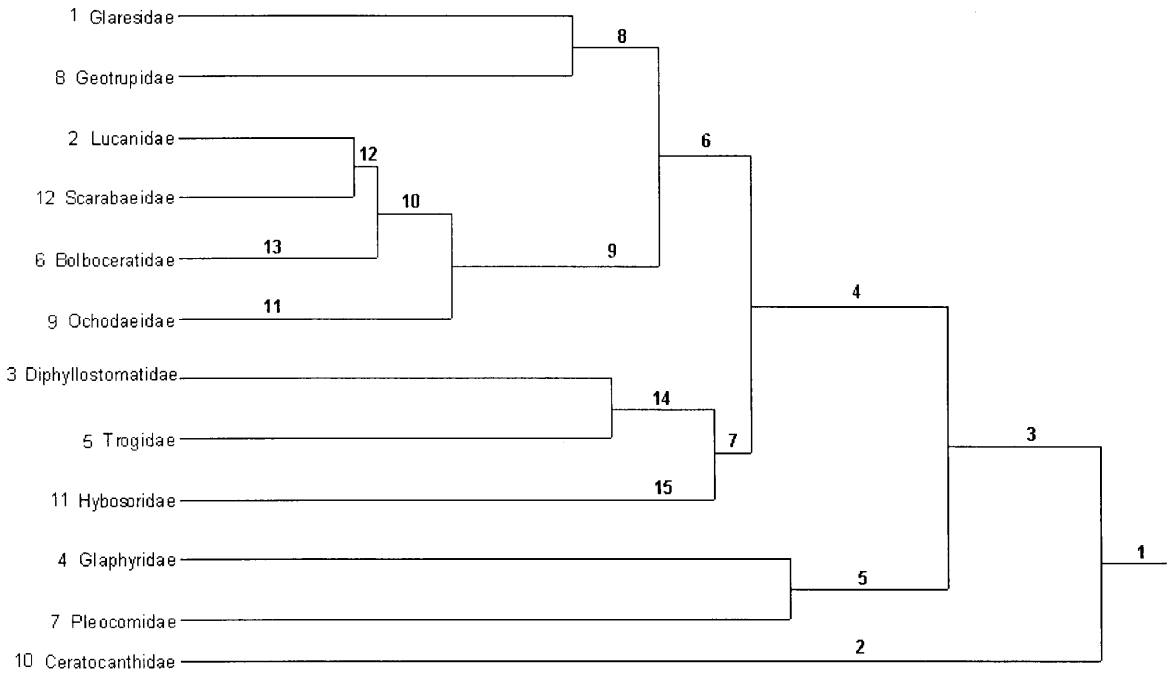


Fig. 10.196 Phenetic tree of the frontal view of metendosternite landmarks compiled using NTSYS-pc and UPGMA statistical methods on Procrustes distances between the twelve families of Scarabaeoidea.

There are two main clusters present in the frontal view of the 12 studied families of the Scarabaeoidea (Fig. 10.196). The first cluster (cluster 3) consists of all the families, except Ceratocanthidae, that is in a cluster of its own (cluster 2).

Cluster 3 is divided into two again, the first (cluster 4), consisting of Glaresidae, Geotrupidae, Lucanidae, Scarabaeidae, Bolboceratidae, Ochodaeidae, Diphyllostomatidae, Trogidae and Hybosoridae. The second cluster (cluster 5) consists of two families, the Glaphyridae and Pleocomidae.

Within cluster 4 there are two main clusters, the Glaresidae, Geotrupidae, Lucanidae, Scarabaeidae, Bolboceratidae and Ochodaeidae cluster (cluster 6) and the Diphyllostomatidae, Trogidae and Hybosoridae cluster (cluster 7). Diphyllostomatidae and Trogidae form cluster 14 in cluster 7 with Hybosoridae in a cluster of its own (cluster 15).

Glaresidae and Geotrupidae (cluster 8) form a loose cluster on its own, while Lucanidae, Scarabaeidae, Bolboceratidae, Ochodaeidae (cluster 9) form another cluster. Cluster 9 is divided into cluster 10 consisting Lucanidae, Scarabaeidae and Bolboceratidae (with Lucanidae and Scarabaeidae forming cluster 11). Cluster 10 is divided into cluster 12 (with Lucanidae and Scarabaeidae) and cluster 13 (consisting only of Ochodaeidae).

In order to try to understand why certain families cluster together in the way they do, the vectors of the landmark positions of families in the "final" clusters, relative to each other, were studied. In the case of the frontal landmark phenogram, the "final" clusters are:

- Glaresidae and Geotrupidae (families 1 and 8),
- Lucanidae and Scarabaeidae (families 2 and 12),
- Diphyllostomatidae and Trogidae (families 3 and 5) and
- Glaphyridae and Pleocomidae (families 4 and 7).

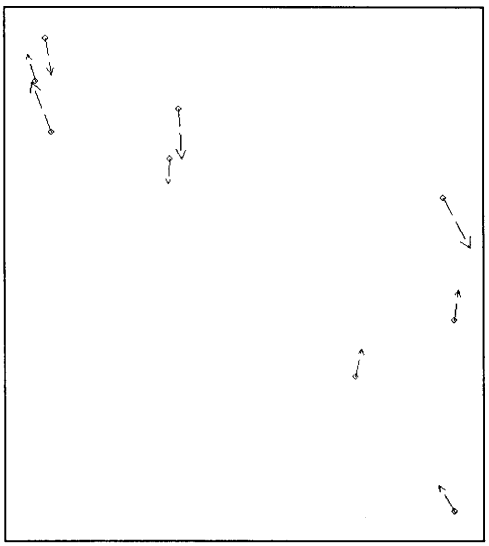


Fig. 10.197 Vector diagram of the frontal view metendosternite landmarks of Glaresidae (represented by the dot) in comparison to landmarks of Geotrupidae (landmark positions situated at arrow head). Vectors represent the differences in landmark positions.

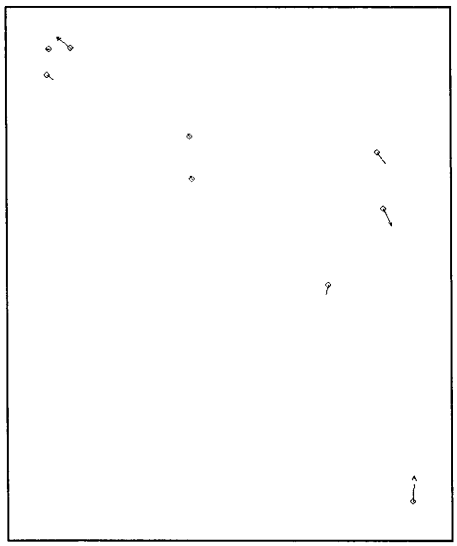


Fig. 10.198 Vector diagram of the frontal view metendosternite landmarks of Lucanidae (represented by the dot) in comparison to landmarks of Scarabaeidae (landmark positions situated at arrow head). Vectors represent the differences in landmark positions.

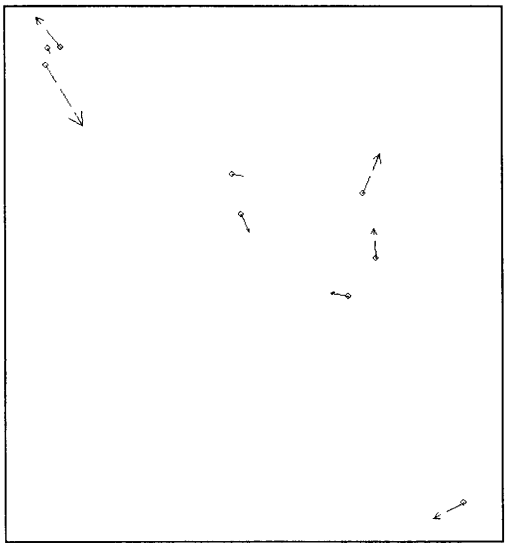


Fig. 10.199 Vector diagram of the frontal view metendosternite landmarks of Diphyllostomatidae (represented by the dot) in comparison to landmarks of Trogidae (landmark positions situated at arrow head). Vectors represent the differences in landmark positions.

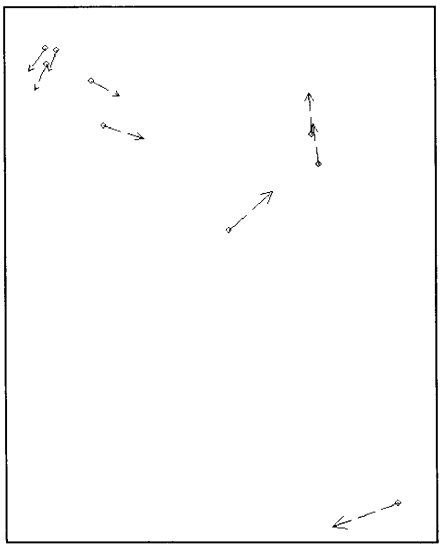


Fig. 10.200 Vector diagram of the frontal view metendosternite landmarks of Glaphyridae (represented by the dot) in comparison to landmarks of Pleocomidae (landmark positions situated at arrow head). Vectors represent the differences in landmark positions.

The differences in positions of the landmarks between one member of the each of the final clusters, compared to the second member, (Fig. 10.197 to 10.200) indicate that there are small differences between the landmark positions of each of the two taxa.

If the phylogeny of the groups are taken into account, Lucanidae, is phylogenetically one of the most primitive Scarabaeoidea. Phenetically, however, Lucanidae is clustered together with Scarabaeidae, the most derived family. The form and shape of the frontal view of the metendosternite of these two families, however, do not vary much (Fig. 10.198). The phenogram placement is totally in contrast to all previous cladistic analysis. It should, however, be remembered that we are analysing shape and landmark positions, not phylogenetic relationships.

In order to try to find phenetic reasons why phylogenetically primitive taxa like the Glaresidae, Diphyllostomatidae and Lucanidae are not situated close to one another on the phenogram, the vector distributions of their landmarks were studied. The overall distribution of the landmarks vary a lot, and that is why they are placed far apart in the phenogram (Fig. 10.201 and Fig. 10.202). Glaresidae and Lucanidae are closer on the phenogram than Glaresidae and Diphyllostomatidae - the landmark positions of Glaresidae compared to Lucanidae therefore vary more that that of Glaresidae compared to Diphyllostomatidae.

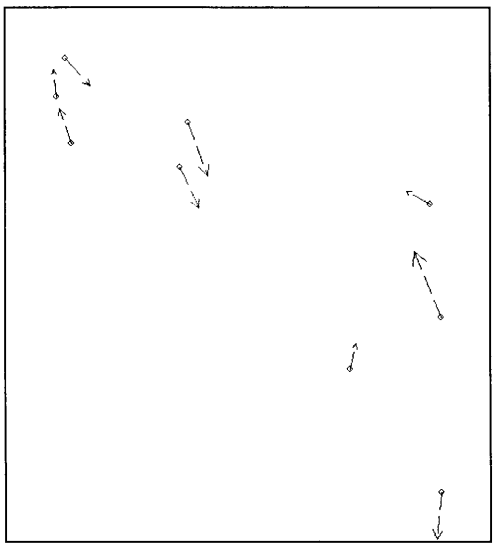


Fig. 10.201 Vector diagram of the frontal view metendosternite landmarks of Glaresidae (represented by the dot) in comparison to landmarks of Lucanidae (landmark positions situated at arrow head). Vectors represent the differences in landmark positions.

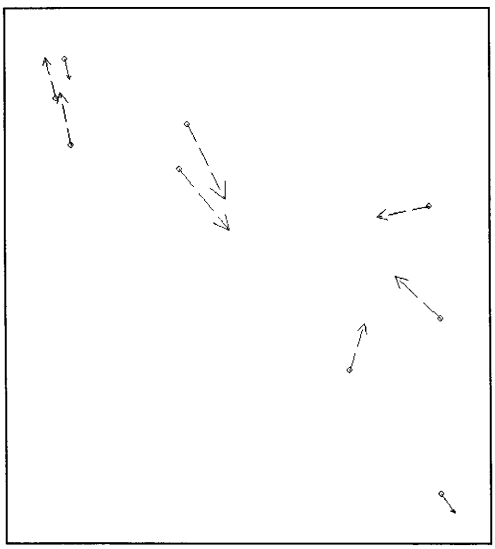


Fig. 10.202 Vector diagram of the frontal view metendosternite landmarks of Glaresidae (represented by the dot) in comparison to landmarks of Diphyllostomatidae (landmark positions situated at arrow head). Vectors represent the differences in landmark positions.

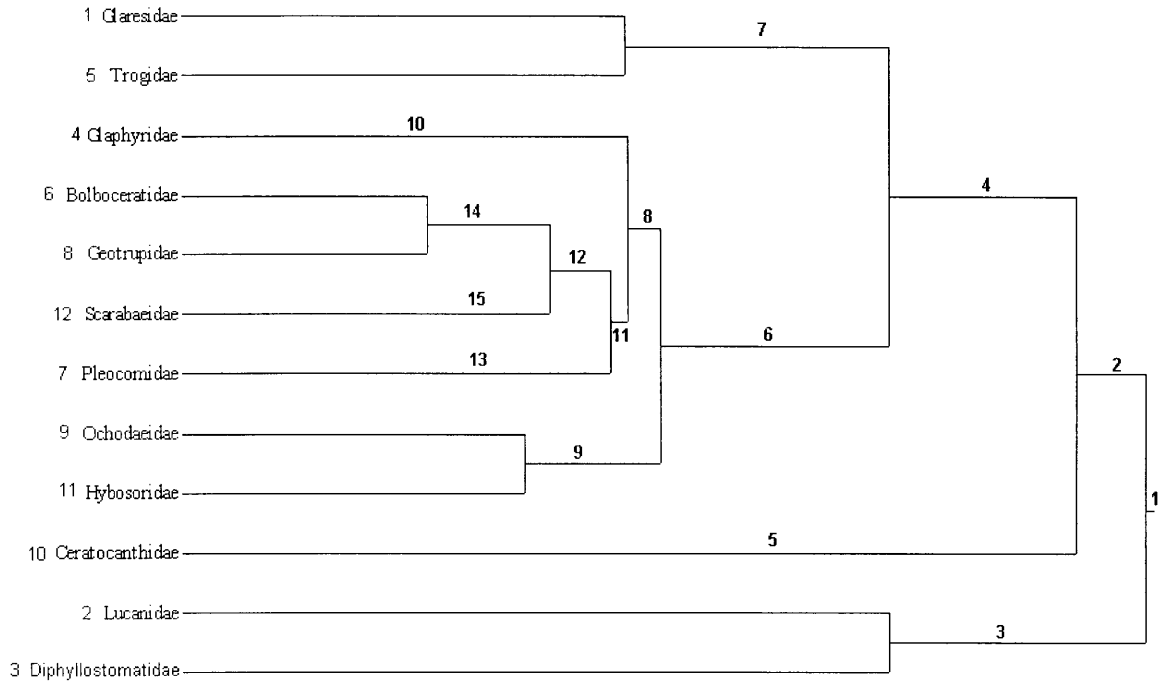


Fig. 10.203 Phenetic tree of the dorsal view of metendosternite landmarks compiled using NTSYS-pc and UPGMA statistical methods on Procrustes distances between the twelve families of Scarabaeoidea.

Two main clusters (clusters 2 and 3) are visible in the dorsal landmark phenogram (Fig. 10.203) of the Scarabaeoidea families, consisting of the Glaresidae, Trogidae, Glaphyridae, Bolboceratidae, Geotrupidae, Scarabaeidae, Pleocomidae, Ochodaeidae, Hybosoridae and Ceratocanthidae (cluster 2), and the Lucanidae and Diphyllostomatidae cluster (cluster 3).

Cluster 2 is divided into two again (cluster 4 and 5), consisting of all the above mentioned families in cluster 4, except Ceratocanthidae that is on its own in cluster 5. Cluster 4 is divided into the Glaresidae and Trogidae cluster (cluster 7) and the Glaphyridae, Bolboceratidae, Geotrupidae, Scarabaeidae, Pleocomidae, Ochodaeidae and Hybosoridae cluster (cluster 6). Cluster 6 is divided into the Glaphyridae, Bolboceratidae, Geotrupidae, Scarabaeidae and Pleocomidae cluster (cluster 8) and the Ochodaeidae and Hybosoridae cluster (cluster 9). Bolboceratidae and Geotrupidae (cluster 14) form a cluster within cluster 8.

There are four "final" clusters within this phenogram:

- Lucanidae and Diphyllostomatidae (families 1 and 2),
- Glaresidae and Trogidae (families 1 and 5),
- Ochodaeidae and Hybosoridae (families 9 and 11) and
- Bolboceratidae and Geotrupidae (families 6 and 8).

The vector distribution of the landmarks of the families in the final clusters (Fig. 10. 204 to 10.207) are arranged very closely, as was the case in the frontal view final clusters.

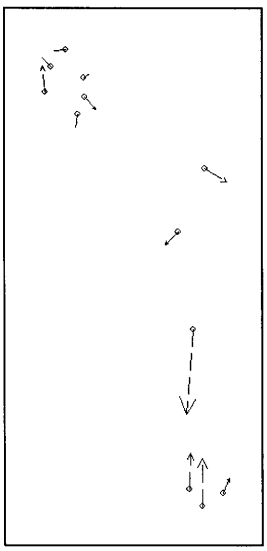


Fig. 10.204 Vector diagram of the dorsal view metendosternite landmarks of Lucanidae (represented by the dot) in comparison to landmarks of Diphyllostomatidae (landmark positions situated at arrow head). Vectors represent the differences in landmark positions.

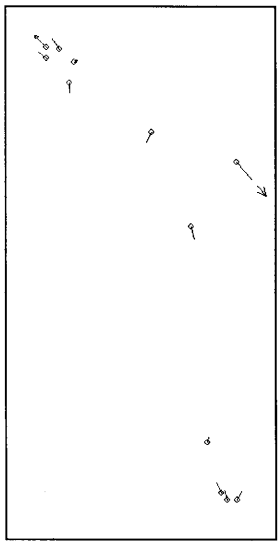


Fig. 10.205 Vector diagram of the dorsal view metendosternite landmarks of Glaresidae (represented by the dot) in comparison to landmarks of Trogidae (landmark positions situated at arrow head). Vectors represent the differences in landmark positions.

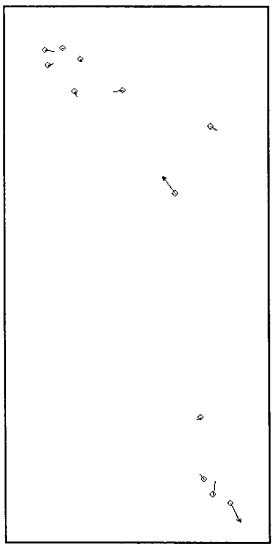


Fig. 10.206 Vector diagram of the dorsal view metendosternite landmarks of Ochodaeidae (represented by the dot) in comparison to landmarks of Hybosoridae (landmark positions situated at arrow head). Vectors represent the differences in landmark positions.

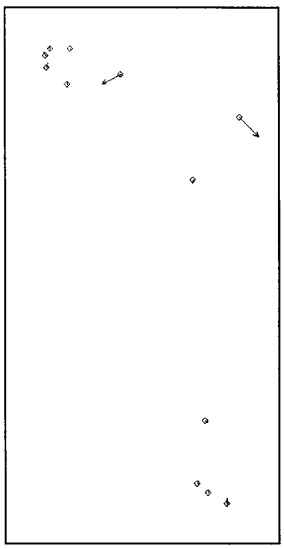


Fig. 10.207 Vector diagram of the dorsal view metendosternite landmarks of Bolboceratidae (represented by the dot) in comparison to landmarks of Geotrupidae (landmark positions situated at arrow head). Vectors represent the differences in landmark positions.

The vector distributions of the landmarks of the three phylogenetically primitive taxa (Glaresidae, Diphyllostomatidae and Lucanidae) were once again compared. These families are not situated close to one another on the phenogram. Fig. 10.208 represents the landmark positions of Lucanidae relative to that of Glaresidae, and Fig. 10.209 represents the landmark positions of Glaresidae relative to Diphyllostomatidae. The Lucanidae and Diphyllostomatidae are placed as a terminal cluster by the dorsal view phenogram, and therefore agrees with the cladogram placement of Browne & Scholtz (1995; in press), also placing them as terminal taxa.

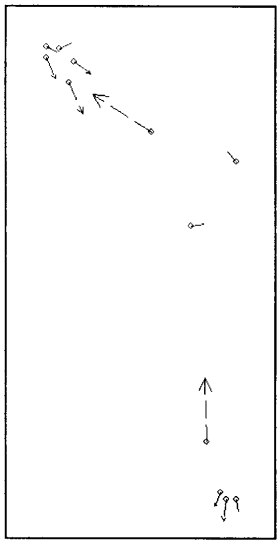


Fig. 10.208 Vector diagram of the dorsal view metendosternite landmarks of Glaresidae (represented by the dot) in comparison to landmarks of Lucanidae (landmark positions situated at arrow head). Vectors represent the differences in landmark positions.

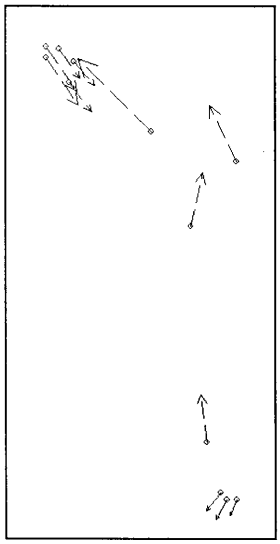


Fig. 10.209 Vector diagram of the dorsal view metendosternite landmarks of Glaresidae (represented by the dot) in comparison to landmarks of Diphyllostomatidae (landmark positions situated at arrow head). Vectors represent the differences in landmark positions.

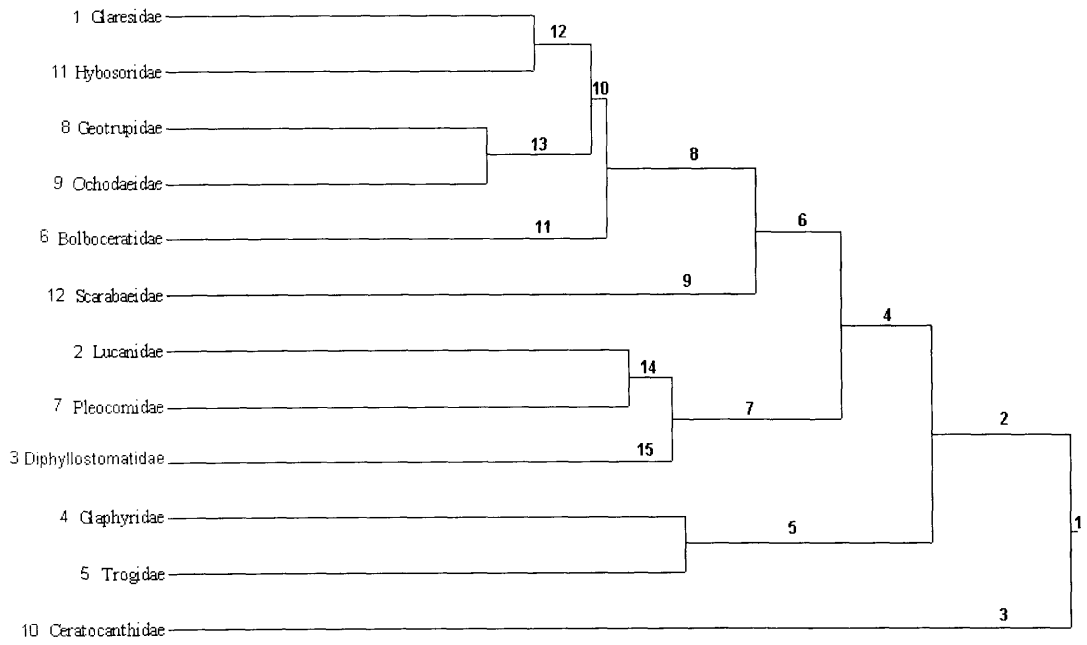


Fig. 10.210 Phenetic tree of the lateral view of metendosternite landmarks compiled using NTSYS-pc and UPGMA statistical methods on Procrustes distances between the twelve families of Scarabaeoidea.

Two main clusters (cluster 2 and 3) are present in the lateral view phenogram of the families of Scarabaeoidea (Fig. 10.210) the first consisting of all the families (cluster 2) except Ceratocanthidae (cluster 3), that is in a cluster of its own. Cluster 2 is divided into the Glaresidae, Hybosoridae, Geotrupidae, Ochodaeidae, Bolboceratidae Scarabaeidae, Lucanidae, Pleocomidae and Diphyllostomatidae (cluster 4) cluster and the Glaphyridae and Trogidae cluster (cluster 5).

Cluster 4 is divided into the Glaresidae, Hybosoridae, Geotrupidae, Ochodaeidae, Bolboceratidae and Scarabaeidae cluster (cluster 5) and the Lucanidae, Pleocomidae and Diphyllostomatidae cluster (cluster 7). Lucanidae and Pleocomidae form a cluster (cluster 14) within the Lucanidae, Pleocomidae and Diphyllostomatidae cluster (cluster 7). Glaresidae, Hybosoridae, Geotrupidae, Ochodaeidae and Bolboceratidae form a cluster (cluster 10), with Scarabaeidae in a cluster of its own (cluster 9). Glaresidae and Hybosoridae form a cluster (cluster 12), Geotrupidae and Ochodaeidae form a cluster (cluster 13) and Bolboceratidae is on its own in a cluster (cluster 11).

The "final" clusters are:

- Glaresidae and Hybosoridae (families 1 and 11),
- Geotrupidae and Ochodaeidae (families 8 and 9),
- Lucanidae and Pleocomidae (families 2 and 7) and
- Glaphyridae and Trogidae (families 4 and 5).

The vector distribution of the landmarks of the families in the final clusters is also arranged very closely, as was the case with the final clusters of the previous two views (Fig. 10.211 to 10.214).

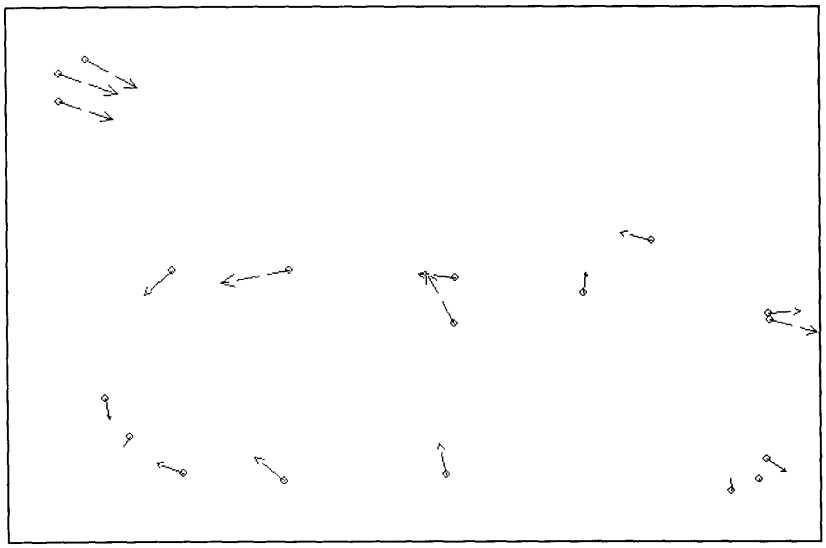


Fig. 10.211 Vector diagram of the lateral view metendosternite landmarks of Glaresidae (represented by the dot) in comparison to landmarks of Hybosoridae (landmark positions situated at arrow head). Vectors represent the differences in landmark positions.

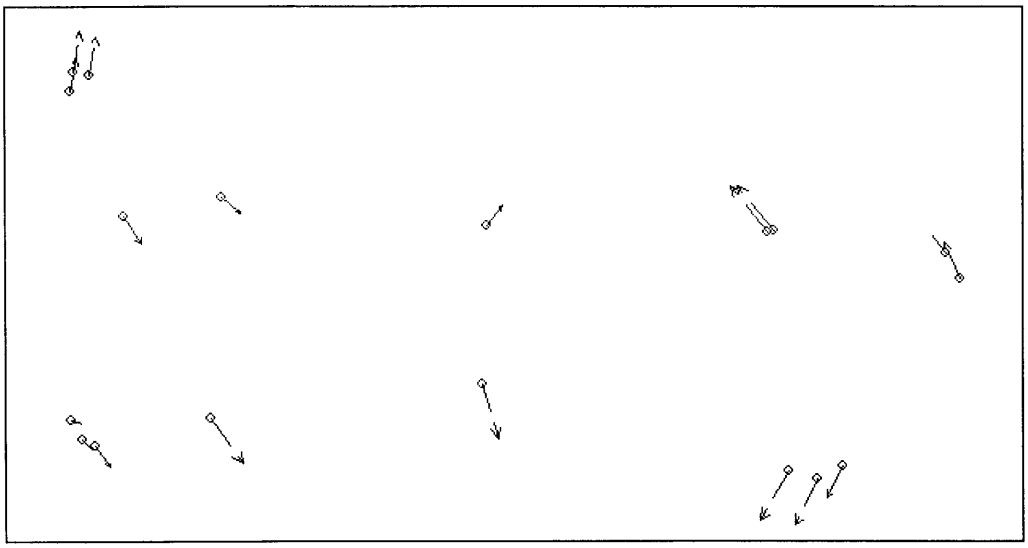


Fig. 10.212 Vector diagram of the lateral view metendosternite landmarks of Geotrupidae (represented by the dot) in comparison to landmarks of Ochodaeidae (landmark positions situated at arrow head). Vectors represent the differences in landmark positions.

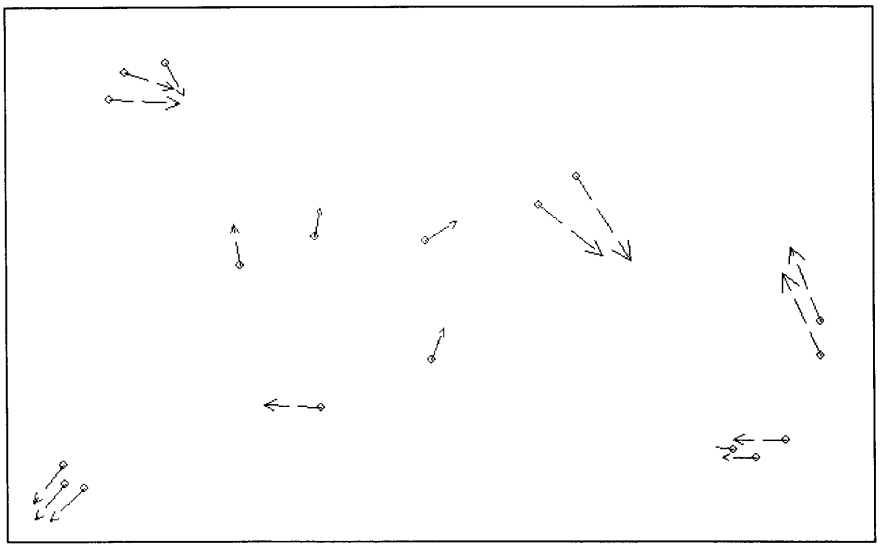


Fig. 10.213 Vector diagram of the lateral view metendosternite landmarks of Glaresidae (represented by the dot) in comparison to landmarks of Diphyllostomatidae (landmark positions situated at arrow head). Vectors represent the differences in landmark positions.

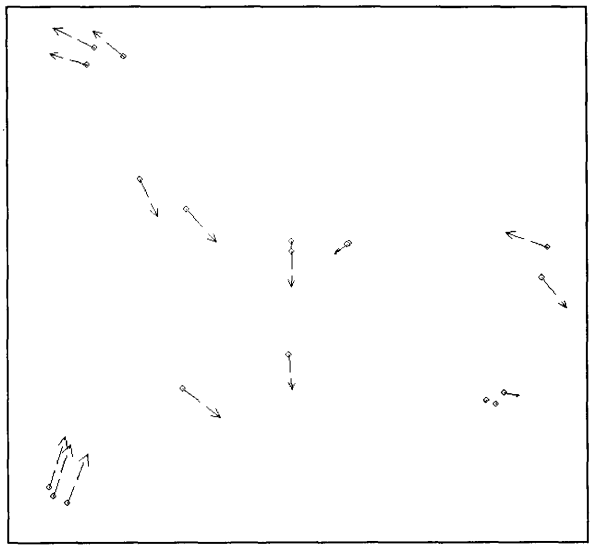


Fig. 10.214 Vector diagram of the lateral view metendosternite landmarks of Glaphyridae (represented by the dot) in comparison to landmarks of Trogidae (landmark positions situated at arrow head). Vectors represent the differences in landmark positions.

Landmark positions of the three primitive taxa (Glaresidae, Diphyllostomatidae and Lucanidae) were once again compared. These taxa are not situated close to one another on the phenogram. Fig. 10.215 represents the landmark positions of Lucanidae relative to that of Glaresidae, and Fig. 10.216 represents the landmark positions of Glaresidae relative to Diphyllostomatidae. Lucanidae and Diphyllostomatidae are situated in the same cluster (cluster 7) of the lateral view phenogram.

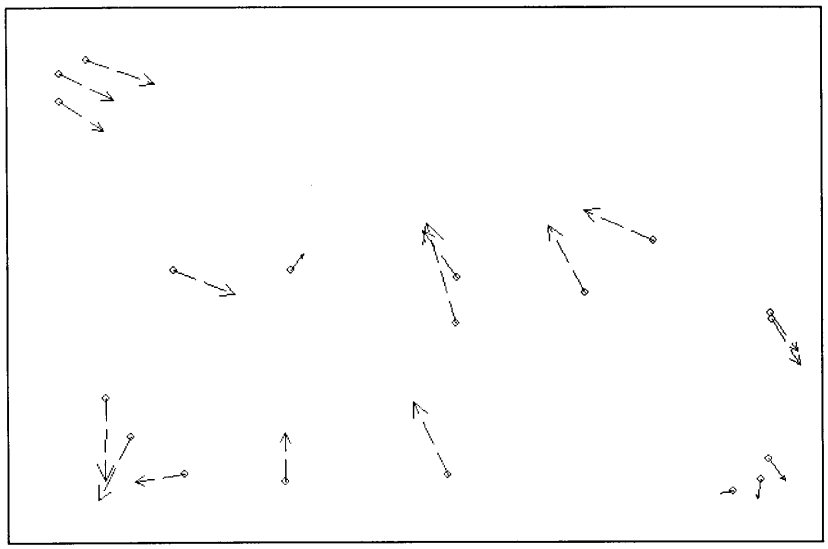


Fig. 10.215 Vector diagram of the lateral view metendosternite landmarks of Glaresidae (represented by the dot) in comparison to landmarks of Lucanidae (landmark positions situated at arrow head). Vectors represent the differences in landmark positions.

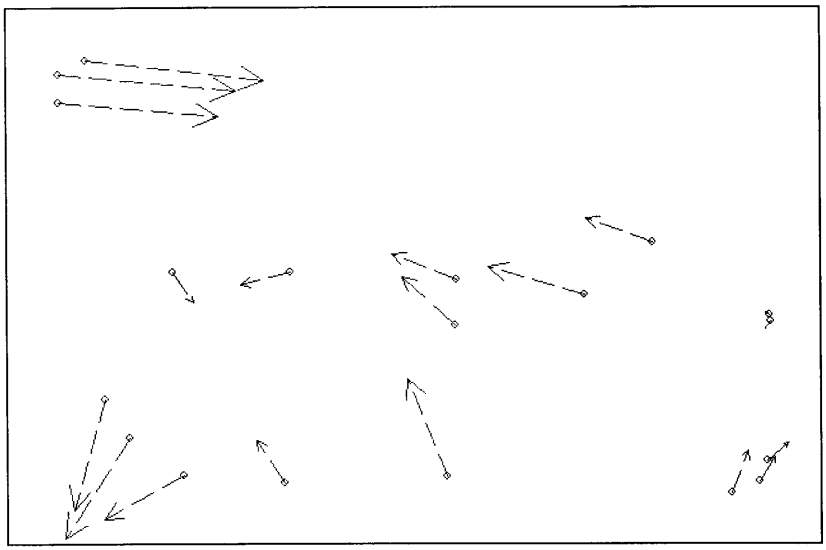


Fig. 10.216 Vector diagram of the lateral view metendosternite landmarks of Glaresidae (represented by the dot) in comparison to landmarks of Diphyllostomatidae (landmark positions situated at arrow head). Vectors represent the differences in landmark positions.

The phenetic placement of the subfamilies of the Scarabaeidae was also studied. Figures 10.217 – 10.219 represent the phenograms of these subfamilies.

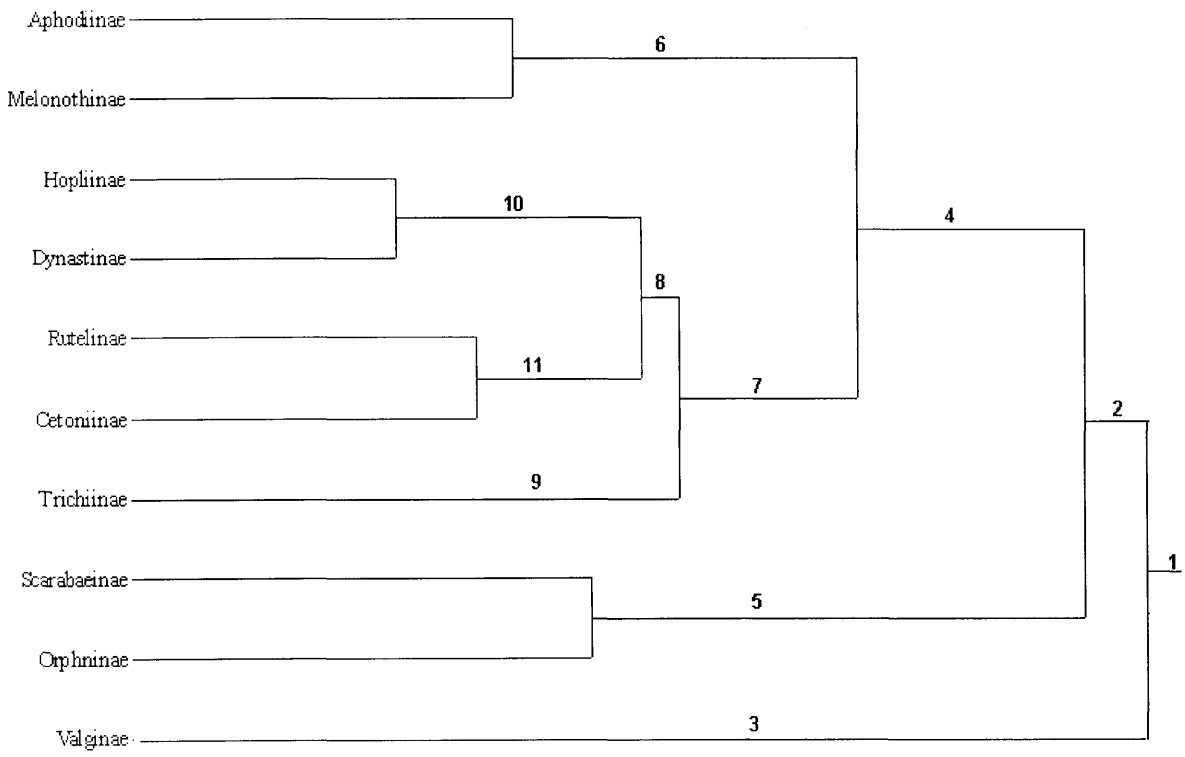


Fig. 10.217 Phenetic tree of the frontal view of metendosternite landmarks compiled using NTSYS-pc and UPGMA statistical methods on Procrustes distances between the 10 studied Scarabaeidae subfamilies.

There are two main clusters in the frontal view phenogram of the subfamilies of the Scarabaeidae (Fig. 10.217) the first (cluster 2) with all subfamilies except Valginae present in cluster 3. Cluster 2 is divided into the Aphodiinae, Melolonthinae, Hopliinae, Dynastinae, Rutelinae, Cetoniinae and Trichiinae cluster (cluster 4) and the Scarabaeinae and Orphninae cluster (cluster 5).

Cluster 4 is divided into the Aphodiinae and Melolonthinae cluster (cluster 6) and the Hopliinae, Dynastinae, Rutelinae, Cetoniinae and Trichiinae cluster (cluster 7). Cluster 7 is divided into the Hopliinae, Dynastinae, Rutelinae and Cetoniinae cluster (cluster 8), with Trichiinae in a cluster of its own (cluster 9). Hopliinae and Dynastinae are in cluster 10 and Rutelinae and Cetoniinae are in cluster 11.

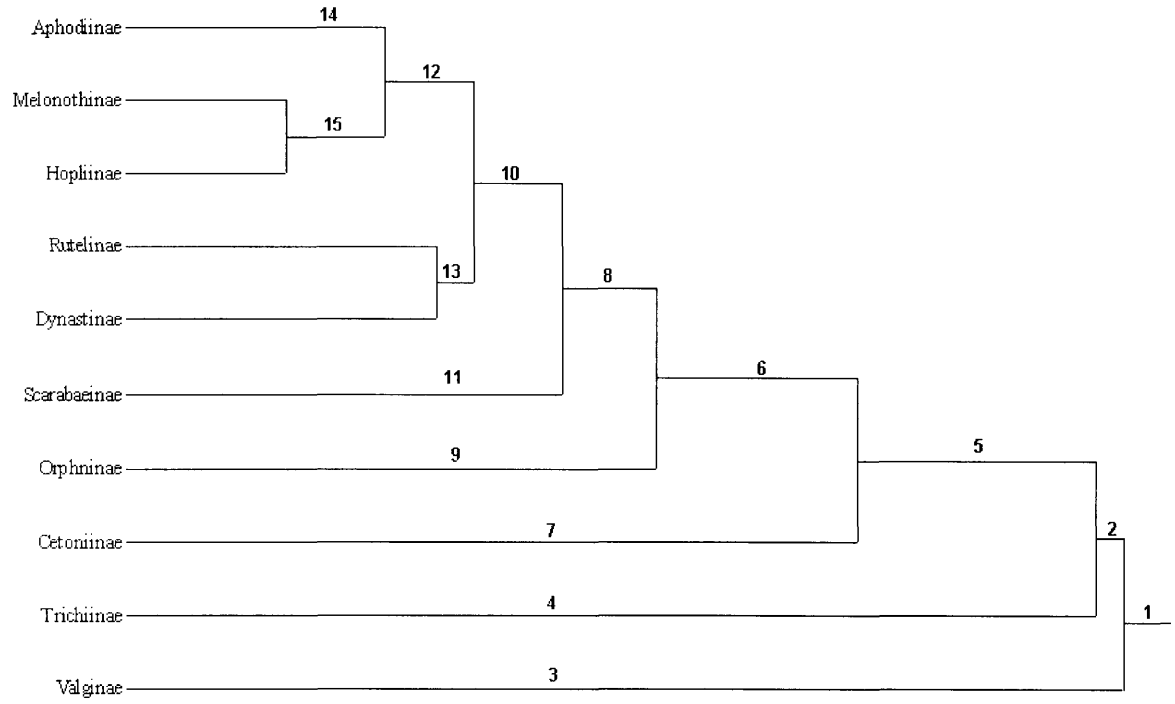


Fig. 10.218 Phenetic tree of the dorsal view of metendosternite landmarks compiled using NTSYS-pc and UPGMA statistical methods on Procrustes distances between the 10 studied Scarabaeidae subfamilies.

There are two main clusters in the dorsal view phenogram of the subfamilies of the Scarabaeidae (Fig. 10.218), cluster 2 contains all the subfamilies except Valginae (cluster 3). Cluster 2, consisting of Aphodiinae, Melolonthinae, Hopliinae, Rutelinae, Dynastinae, Scarabaeinae, Orphninae, Cetoniinae and Trichiinae is divided into clusters 4 and 5. Trichiinae is the only taxon in cluster 4. The Aphodiinae, Melolonthinae, Hopliinae, Rutelinae, Dynastinae, Scarabaeinae, Orphninae and Cetoniinae cluster (cluster 5) is divided into two clusters, the first (cluster 6) consisting of all the taxa except Cetoniinae (found in cluster 7). The Aphodiinae, Melolonthinae, Hopliinae, Rutelinae, Dynastinae, Scarabaeinae and Orphninae cluster (cluster 6) is divided into clusters 8 and 9. Only Orphninae is present in cluster 9. Cluster 8 is divided into cluster 10 and 11, with cluster 11 only consisting of Scarabaeinae (cluster 11). The Aphodiinae, Melolonthinae, Hopliinae, Rutelinae and Dynastinae (cluster 10) is divided into clusters 12 and 13. Aphodiinae, Melolonthinae and Hopliinae is present in cluster 12 and cluster 13 consists of Rutelinae and Dynastinae. Cluster 12 is divided into the Melolonthinae and Hopliinae cluster (cluster 15) and Aphodiinae in a cluster of it's own (cluster14).

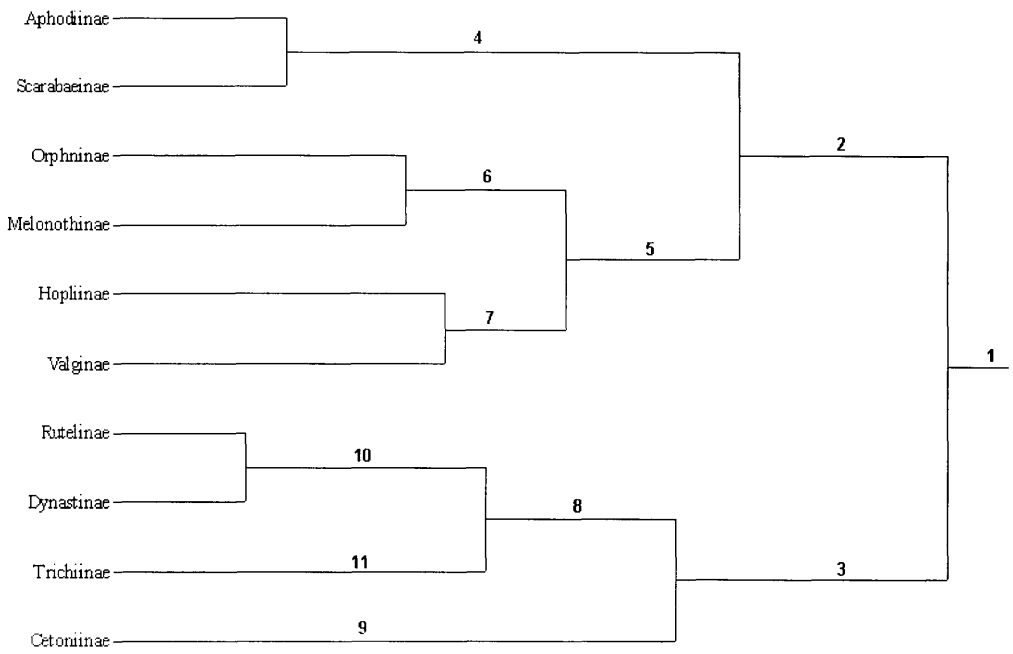


Fig. 10.219 Phenetic tree of the lateral view of metendosternite landmarks compiled using NTSYS-pc and UPGMA statistical methods on Procrustes distances between the 10 studied Scarabaeidae subfamilies.

There are two main clusters (cluster 2 and 3) in the lateral view phenogram of the subfamilies of Scarabaeidae (Fig. 10.219). Cluster 2 consists of Aphodiinae, Scarabaeinae, Orphninae, Melolonthinae, Hopliinae and Valginae while cluster 3 consists of Rutelinae, Dynastinae, Trichiinae and Cetoniinae.

Cluster 2 is divided into the Aphodiinae and Scarabaeinae cluster (cluster 4) and the Orphninae, Melolonthinae, Hopliinae and Valginae cluster (cluster 5). Orphninae and Melolonthinae (cluster 6) and Hopliinae and Valginae (cluster 7) form two clusters.

Cluster 3 is divided into the Rutelinae, Dynastinae and Trichiinae cluster (cluster 8) with Cetoniinae in a cluster of its own (cluster 9). Rutelinae and Dynastinae are in a very tight cluster of their own (cluster 10), with Trichiinae alone in cluster 11.

The frontal and dorsal view landmark phenograms are very close to one another, but the lateral view phenogram is probably resembles the predicted phylogeny of the family most

closely (Scholtz, personal communication). At this stage there is no comprehensive cladogram of the family to which the phenograms can be compared. The consensus configuration of the landmark positions of all the subfamilies, were generated by the tps series of programs and used in the data that produced the phenograms of thefamilies of the Scarabaeoidea.

RELATIVE WARP ANALYSIS OF THE THREE VIEWS OF THE METENDOSTERNITES OF THE SCARABAEOIDEA FAMILIES

The first two relative warps (using á=0) of the frontal view landmarks account for 83.03% of the variation among the specimens. These two relative warps also account for 67.17% variation in the dorsal views and 70.35% variation in the lateral views (this is based on a matrix of singular values from a singular-value decomposition of the weight matrix (Rohlf, 1993b).

Table 10.2 A, B and C represents the singular values and percentage variation attributed to each relative warp. If the first two relative warps of each of the three views are plotted against each other, an idea can be formed of which metendosternite forms are closerto one another, by looking at the placements of the families on the two axes. Fig. 10.220, 10.223 and 10.227 respectively show a two-dimensional ordination of the overall diversity (relative warp 1 (*x*-axis) plotted against relative warp 2 (*y*-axis)) of the 12 families in terms of their non-affine components of shape variation for each of the three metendosternite views. The tpsRelw program (as mentioned previously) was used to explore the changes in shape corresponding to different positions in the ordinations. It is possible to view the splines of taxa situated closely together on the ordination and to visually establish, because of the relative positions of certain landmarks, why these taxa are grouped closely together.

Table 10.2A Singular values and percent explained for relative warps of the frontal views

Rel.W	Singular value	%
1	0.51113	60.23%
2	0.31451	22.80%
3	0.17665	7.19%
4	0.13538	4.23%
5	0.10252	2.42%
6	0.09262	1.98%
7	0.05469	0.69%
8	0.03915	0.35%
9	0.01835	0.08%
10	0.00823	0.02%
11	0.00647	0.01%

Table 10.2B Singular values and percent explained for relative warps for the dorsal views

Rel.W	Singular value	%
1	0.24540	48.62%
2	0.15159	18.55%
3	0.15021	18.22%
4	0.09455	7.22%
5	0.06701	3.63%
6	0.04132	1.38%
7	0.04043	1.32%
8	0.02288	0.42%
9	0.01993	0.32%
10	0.01719	0.24%
11	0.01019	0.08%

Table 10.2C Singular values and percent explained for relative warps of the lateral view

Rel.W	Singular value	%
1	0.45420	52.08%
2	0.26904	18.27%
3	0.24540	15.20%
4	0.13426	4.55%
5	0.12667	4.05%
6	0.09112	2.10%
7	0.07153	1.29%
9	0.04588	0.53%
10	0.02934	0.22%
11	0.02539	0.16%

RELATIVE WARP I AND 2 OF THE FRONTAL VIEW

The distribution of families on this plot (Fig. 10.220) follows the same pattern as represented in the frontal view phenogram. The families are scattered relatively widely apart on the plot, but definite groupings are visible. Glaresidae and Geotrupidae (families 1 and 8) are relatively close to each other on the scatter plot. This is also the case in the phenogram, where Glaresidae and Geotrupidae are clustered together, forming a terminal cluster. Lucanidae, Scarabaeidae and Bolboceratidae (families 2, 12 and 6) are placed relatively close to one another, with Ochodaeidae (family 9) also near this cluster. The same clustering is present in the phenogram (these four families are situated on cluster 9). Diphyllostomatidae and Trogidae (families 3 and 5) are situated close on the scatter plot, and these two families form a terminal cluster on the phenogram (cluster 14), with Hybosoridae (family 11, cluster 15) grouped together in a cluster (cluster 7) with Diphyllostomatidae and Trogidae.

Glaphyridae and Pleocomidae (families 4 and 7) form a terminal cluster on the phenogram (cluster 5) and they are clustered relatively far away from each other, but with no other family in their immediate vicinity on the relative warp 1 and 2 plot. Shape changes between these two families, shown as deformations of the reference configuration (using thin-plate splines produced by tpsRelw) indicate little variation, and one can establish the exact landmarks responsible for the differences between the taxa. Splines of Lucanidae, Bolboceratidae, Scarabaeidae and Ochodaeidae (families 2, 6, 12 and 9) are shown in Fig.10.221 A to D. The spline of Scarabaeidae (family 12) (Fig. 10.221C) is also the closest to the reference configuration of landmarks (as it is situated the closest to the origin on the scatter plot, and the origin represents the reference configuration), and it's spline shows the least deformation.

Fig. 10.222A and B are thin-plate splines of Diphyllostomatidae and Trogidae respectively to indicate the shape changes as deformations. The thin-plate splines are very similar, these two families are situated quite close on the plot, and form a terminal cluster (cluster 5) on the phenogram (Fig. 10.196).

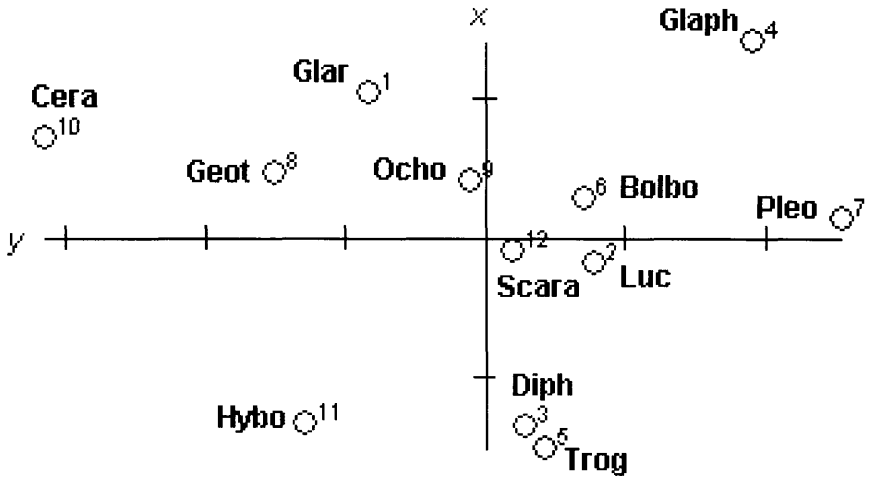


Fig. 10.220 Relative warp I (*x*-axis) and 2 (*y*-axis) computed from the frontal view data set, plotted against one another to indicate positions of the families relative to one another and to the reference configuration (situated at the origin). These two relative warps represent 83.03% of the variation between families.

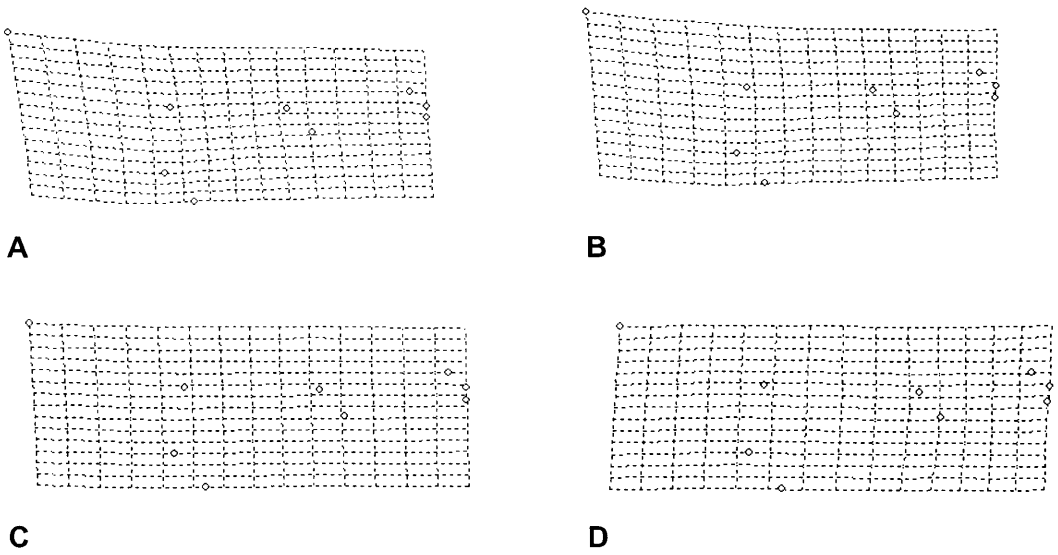
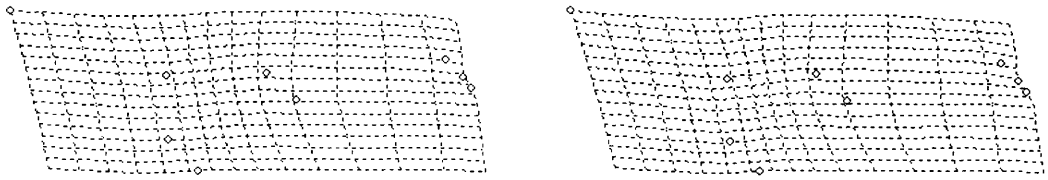


Fig.10.221 Shape change implied by variation along the first two relative warp axes. Shape changes are shown as deformations using thin-plate splines. A, Lucanidae; B, Bolboceratidae; C, Scarabaeidae and D, Ochodaeidae (GLS reference used). Frontal view data set.



A B

Fig.10.222 Shape change implied by variation along the first two relative warp axes. Shape changes are shown as deformations using thin-plate splines. A, Diphyllostomatidae and B, Trogidae. (GLS reference used). Frontal view data set.

RELATIVE WARP I AND 2 OF THE DORSAL VIEW

The scatter plot of relative warp 1 plotted against 2 of the dorsal view data set of the Scarabaeoidea families (Fig. 10.223) also coincides with the respective phenogram (Fig. 10.203). Families Scarabaeidae, Geotrupidae, Bolboceratidae (cluster 12) and Hybosoridae (cluster 9) appear close on the phenogram and also close on the scatter plot (Fig. 10.223).

Lucanidae and Diphyllostomatidae (appearing as a terminal cluster on cluster 3 of the phenogram) are situated relatively far apart on the scatter plot of relative warp 1 and 2, there are, however, no other families situated close to them. Shape changes between these two families are represented as deformations using thin-plate splines (Fig. 10.226). The general trend of the landmark positions of the two families is the same, and no other landmark distribution is comparable with them.

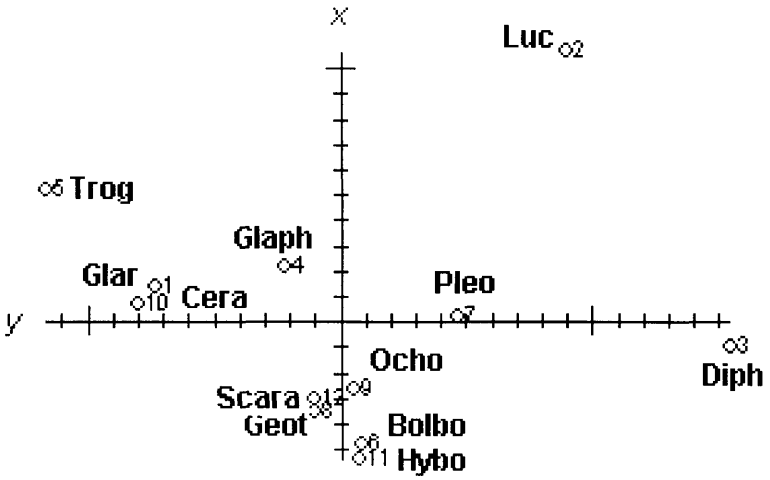
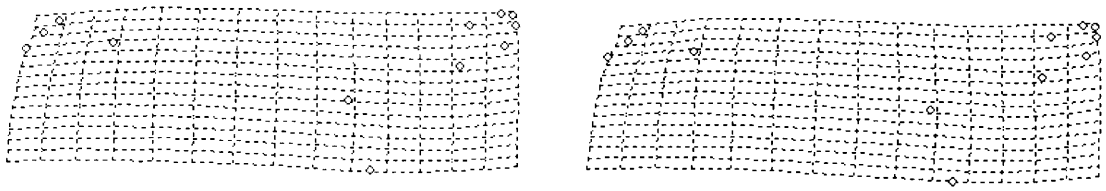
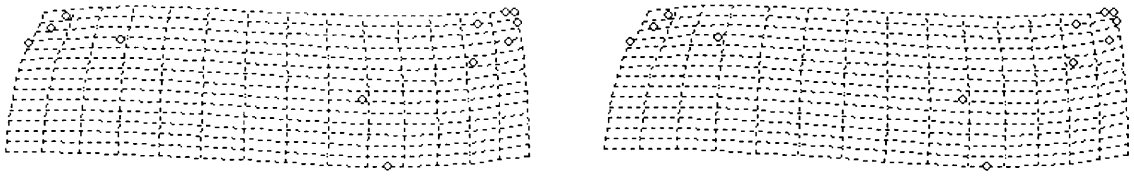


Fig. 10.223 Relative warp I (x-axis) and 2 (y-axis) computed from the dorsal view data set, plotted against one another to indicate positions of the families relative to one another and to the reference configuration (situated at the origin). These two relative warps represent 67.17% of the variation between families.



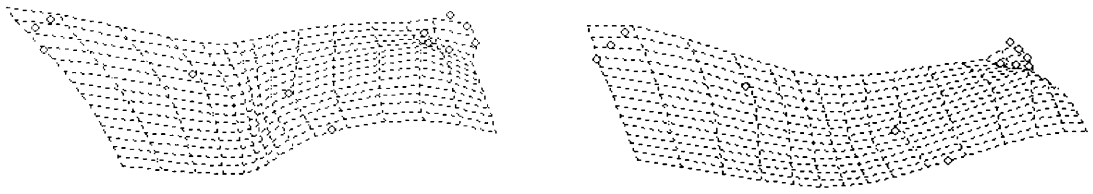
A **B**

Fig.10.224 Shape change implied by variation along the first two relative warp axes. Shape changes are shown as deformations using thin-plate splines. A, Scarabaeidae and B, Geotrupidae. (GLS reference used). Dorsal view data set.



A B

Fig.10.225 Shape change implied by variation along the first two relative warp axes. Shape changes are shown as deformations using thin-plate splines. A, Bolboceratidae and B, Hybosoridae (GLS reference used). Dorsal view data set.



A B

Fig.10.226 Shape change implied by variation along the first two relative warp axes. Shape changes are shown as deformations using thin-plate splines. A, Lucanidae and B, Diphyllostomatidae. (GLS reference used). Dorsal view data set.

RELATIVE WARP I AND 2 OF THE LATERAL VIEW

Relative warp 1 plotted against 2 of the lateral view data set of the Scarabaeoidea families also coincides with the respective phenogram (Fig. 10.210). Glaresidae, Ochodaeidae, Hybosoridae and Geotrupidae appear relatively close to one another on the scatter plot (Fig. 10.227). These families also appear on cluster 10 of the phenogram. Shape changes shown as deformations of thin-plate splines of these four families are shown in Fig 10.228A to D.

Lucanidae, Pleocomidae and Diphyllostomatidae also appear close on the scatter plot (Fig. 10.227). These families are grouped together in a cluster (cluster 15) of the phenogram. Shape changes as deformations of thin-plate splines of the three families are shown in Fig, 10.229A to C.

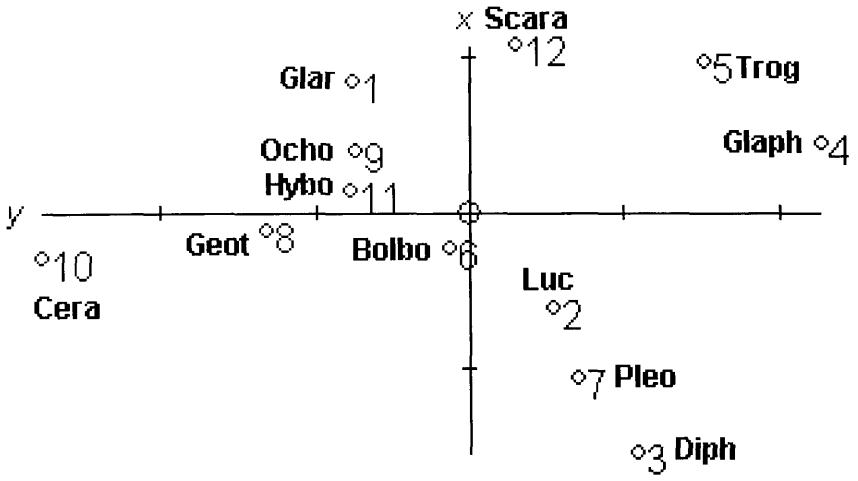


Fig. 10.227 Relative warp I (x-axis) and 2 (y-axis) computed from the lateral view data set, plotted against one another to indicate positions of the families relative to one another and to the reference configuration (situated at the origin). These two relative warps represent 83.03% of the variation between families.

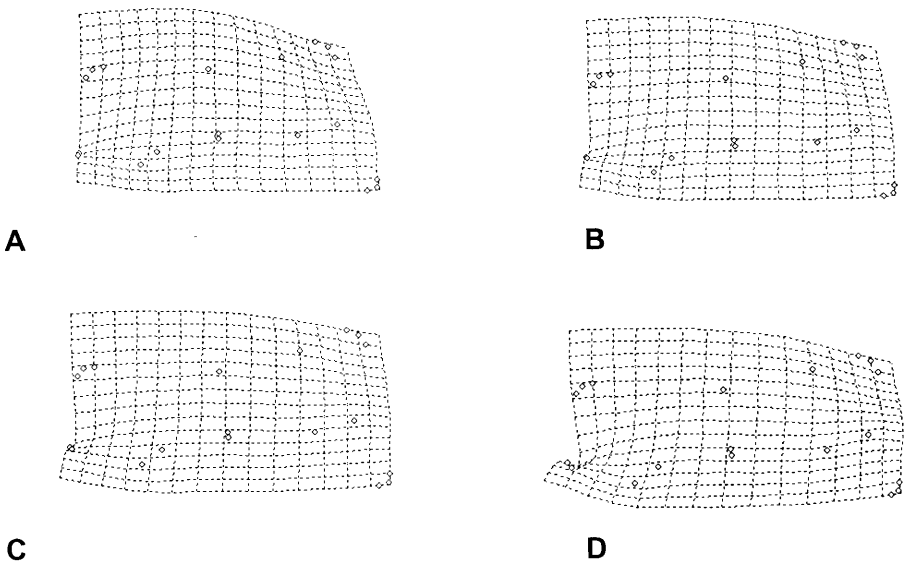
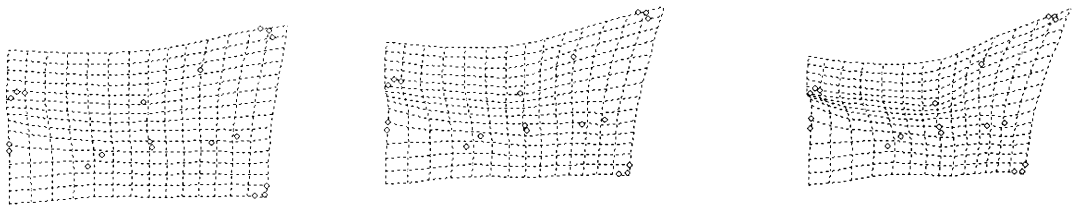


Fig.10.228 Thin-plate spline of relative warp 1 and 2 of A, Glaresidae; B, Ochodaeidae; C, Hybosoridae and D Geotrupidae. (GLS reference used). Lateral view data set.



A B C

Fig.10.229 Thin-plate spline of relative warp 1 and 2 of A, Lucanidae; B, Pleocomidae and C, Diphyllostomatidae. (GLS reference used).

DISCUSSION

As mentioned earlier, the Passalidae were not included in the analysis of the metendosternites. Although there can be little doubt about the monophyly of the Scarabaeoidea (Browne & Scholtz, in press) the Passalidae possess a suite of unique adult and larval morphological characters and behavioural traits which have led students of the group to consider them to represent an independent lineage within the superfamily, and to be only distantly related to the other groups.

The family Passalidae, with approximately 40 genera and 500 species (Reyes-Castillo, 1970) is essentially pantropical in distribution (Crowson, 1967). Adult members of the family are usually large, elongated, flattened beetles with distinctly striated elytra. The antennae are curved and the different segments of the antennal club do not fit close together, something that distinguishes them from other scarabaeoids. Larvae are elongate and not typically C-shaped (as are most other scarabaeoid larvae) and their hind legs are reduced to stumps. Adults and larvae are found in decaying hardwood logs where they live in family groups consisting of up to a few dozen individuals. Adults feed the larvae on prepared stomodeal food and assist them in the construction of pupal cocoons (Reyes-Castillo & Halffter, 1984).

Passalidae have traditionally been considered one of the primitive scarabaeoid families (Crowson, 1967, 1981; Reyes-Castillo, 1970; Howden, 1982; Scholtz, 1990; Browne & Scholtz, 1995) but their distinctive combination of plesiomorphic and highly apomorphic characters have historically led to controversy about their phylogenetic placement. However, in spite of reservations expressed in the past about the family's relationships Browne and Scholtz (in press) unequivocally placed it amongst the "primitive" scarabaeoids, as sister-group to a lineage containing the Lucanidae, Diphyllostomatidae, Glaphyridae, Trogidae, Pleocomidae and Bolboceratidae.

The passalid metendosternite (Appendix 10.1) is very different compared to that of any of the other scarabaeoids, resembling rather that of a typical Histeridae most closely. The metendosternite is continuous with the ventral body wall forming a "pipe" dorsally (this is not so in any of the Scarabaeoidea, as the typical other metendosternite is attached by a thin

area at the margin of the thorax and abdomen) (see dorsal views of passalid metendosternites, Appendix 10.1). The beginning of this "pipe" is visible as a hole in the frontal view, but absent in the rest of the taxa (see frontal views of passalid metendosternites, Appendix 10.1). The passalid metendosternite is also more flattened and elongated than a typical scarabaeoid metendosternite. The third pair of legs articulate in sockets (situated in the ventral body wall). These sockets are continuous with the lateral sides of the metendosternite (see lateral views of passalid metendosternites, Appendix 10.1). This similarity in a complex morphological structure between a member of the Scarabaeoidea and one of the Histeroidea implies some additional support for the now largely disused grouping of primitive beetle superfamilies into the Haplogastra. Although there is little evidence to support the Haplogastra (Hydrophiloidea, Staphylinoidea, Histeroidea and Scarabaeoidea) as a monophyletic entity there is general consensus amongst coleopterists that some relationships exist between the various superfamilies. Staphylinoidea are currently considered the most likely sister-group of the Scarabaeoidea although there is also some evidence for Histeroidea being closely related. Close similarity in complex metendosternite structure between Passalidae and Histeridae may indicate stronger relationship than is currently the view.

Because of the doubt about identifying homologous landmarks on the Passalidae metendosternite as compared to those in the other taxa, and because of the clear similarity between passalid and histerid metendosternite structure, it was decided to omit Passalidae from the current study and to investigate this phenomenon in a subsequent study. Although we feel uncomfortable with the greater similarity between these two distantly-related taxa than with more closely related ones we are unable at present to offer an explanation for it.

The metendosternite is one of the internal anatomical structures that has largely been neglected in systematic studies in the past. Exceptions are Crowson (1938, 1944) and Iablokoff-Khnzorian (1977). Crowson (1944) discussed the forms of the metendosternites and together with other morphological characters, philosophised on the possible phylogeny of the Coleoptera. He used the structure of the metendosternites to come to certain phylogenetic conclusions about the families and superfamilies of the Coleoptera. The main purpose of his paper was also to establish the ancestral metendosternite form of the Polyphaga. He named this ancestral furca the Hylecoetoid type and suggested that it is

monophyletic in origin and because of this should be a character of major importance in taxonomy and phylogeny. The present study supports Crowson's theory that the metendosternite may be of taxonomic and phylogenetic importance. If the general form of the metendosternites of each of the families of the Scarabaeoidea (excluding the Passalidae) is examined, general trends are clearly recognisable. It can without prior knowledge of which species (genus or family) it belongs to, be placed in the correct family just by noting these general trends. Crowson's claim of the phylogenetic importance of the structure is consequently apparently substantiated and is therefore accepted, but there is a need to take it further from here. This paper therefore aimed to explore the possibilities of statistically describing the form of these metendosternites.

A question that might be raised from a statistical point of view, is whether the amount of variation among the members of a superfamily is small enough for statistical analysis to be permitted. Because the morphology of members of a superfamily is studied, there will be much more diversity among the structures than is present among species of the same genus. If too much diversity is present in the study group, how will that affect the approximation of shape space? The tpsSmall program in the tps series of programs, can determine the uncentered correlation between the tangent space, regressed onto Procrustes distance (geodesic distances in radians). Analyses using tspSmall of the data sets from the three views, indicated that for all three views of the metendosternites, an excellent correlation between the tangent and the shape space exists. The tangent space is useful in most studies (such as this study) when the shape variation is small, as it allows simpler standard multivariate methods. Geometric morphometric methods are, however, being developed to work directly on shape space, useful when shape variation is not small (personal communication, Rohlf). There is little doubt, on the basis of the results from tpsSmall, that families within a taxon such as a superfamily can be analysed by geometric morphometric methods since the results from the statistical test performed by tspSmall proves the acceptability of the data sets for further statistical analysis.

The question of which reference configuration (used to define the point of tangency between the non-linear shape space and the approximating linear tangent space) should be used for the data sets, has been debated in the past (Swiderski, 1993; Fink & Zelditch, 1995; Rohlf*et al.,* 1996; Adams & Rosenberg, 1998). In order to produce Procrustes distance matrices of

the three views (to produce the different phenograms) the tangent or reference configuration as defined by Rohlf *et al.* (1996) for each of the three data sets should be determined.

The results indicated a good correlation between the scatter plots of the first two relative warps of all three data sets and the respective phenograms (produced from the Procrustes distances). Families clustering together in the phenograms, were closely situated on the scatter plots of the first two relative warps. The scatter plot and phenogram produce the same results, but the scatter plots perhaps more than the phenograms indicate associations "better" between the families of the Scarabaeoidea. This is because clusters are placed relative to each other in a visual way, and relationships are therefore noticed at first glance. PCA ordinations tend to show distant relationships better and cluster analysis tends to show close relationships better. Thus, both are useful and are complementary.

The usefulness of geometric morphometric results in determining evolutionary relationships and whether indeed these results can be used in evolutionary studies has been a speculation point (Adams & Rosenberg, 1998; Rohlf, 1998). Although we tried to compare the results of this geometric morphometric study to those of the results from the cladistic analysis of Browne and Scholtz (in press), there are clearly too many unresolved problems. The cladogram of Browne and Scholtz was based on a phylogenetic analysis of 134 characters, and the most comprehensive up to date. My only conclusion after the comparison, is that there is not enough evidence form the geometric morphometrics study of the metendosternites to indicate evolutionary trends similar to those depicted by the Browne and Scholtz's (in press) cladogram. Similarities between the lateral view phenogram and the cladogram are, however, presented in the following paragraphs. (The lateral view phenogram (Fig. 10.210) and scatter plot (Fig. 10.227) results compare the most favourably to those of their cladogram). The most important reason why the best correlation was obtained between the cladogram and the lateral view phenogram/scatter plot is probably because more landmarks were used in the analysis of the data set that produced the lateral view results of the metendosternites. The lateral view data set consists of 19 landmarks, while fewer landmarks were identified from the dorsal (12 landmarks) and frontal view (9 landmarks). When using more landmarks, more information about the form and structure is gathered (subtle variation differences are then also picked up) and therefore a better

comparison between the variation in the form between members of the data set can be made.)

Browne and Scholtz's cladistic analysis indicated two basal lineages, the glaresid lineage and a second lineage that is divided into two lower level lineages, the passalid and scarabaeid lineages. The passalid lineage contains two lines, the glaphyrid and geotrupid line. The glaphyrid line contains Passalidae, Lucanidae, Diphyllostomatidae, Trogidae, Bolboceratidae, Pleocomidae and Glaphyridae. On the lateral view phenogram (Fig. 10.210), Lucanidae, Pleocomidae and Diphyllostomatidae (cluster 7) form a cluster, while Trogidae and Glaphyridae are in a cluster (cluster 5). These 5 families are loosely grouped together on the relative warp one and two scatter plot. They, however, do not appear together in a direct cluster on the phenogram, as is the case in the clusters of the cladogram.
The geotrupid line of the cladogram contains Geotrupidae, Ochodaeidae, Ceratocanthidae and Hybosoridae. The phenogram cluster, cluster 10 consists of Glaresidae, Hybosoridae, Geotrupidae and Ochodaeidae, while Ceratocanthidae appears in a cluster of its own (cluster 3) and is apparently morphologically quite distinct from the rest of the families. Ceratocanthidae also appears removed from the rest of the families on relative warp one and two lateral view scatter plot, but with the nearest taxa, Geotrupidae, Hybosoridae and Ochodaeidae.

Geometric morphometrics is a powerful tool and its uses in taxonomy, phenetics and even cladistics have not yet been fully explored. I believe that this thesis paves the way for geometric morphometric research on higher level taxa, as it has proved that it can present additional information about the phenetic relationships between taxa of the Scarabaeoidea. Phenetic relationships between taxa have been neglected in the past and many traditional cladists in effect ignored results from phenetic analysis. The main reason perhaps is because evolutionary or phylogenetic relationships are not explicitly sought after in phenetics, but they are nevertheless supposed to be reflected in phenetic classifications (Skelton, 1993).

Because of strong criticism against the lack of subjectivity in phenetic procedures and because a phenogram depicts a hierarchy of relative phenotypic similarity of a set of species, it has not widely been used in phylogenetics (Wiley, 1981; Skelton, 1993). Although I would

have liked the phenogram to reflect the phylogeny of the families, I was unable to do that. But instead of trying to compare cladistic results with the phenetic results of the geometric morphometric analysis, or prove that the one is "better" than the other, the aim of this thesis is to present phenetic results of the first geometric morphometric analysis at family level.

Perhaps geometric morphometrics is the key to re-opening the debate on the usefulness of phenetics, especially in helping to overcome the subjectivity problem. This time around pheneticists have an additional and powerful statistical tool to defend their beliefs, but before we can even start to think about how we can compare and bring phenetics and cladistics together, we must first explore new areas and different possibilities of geometric morphometric analysis. Only after "all" the possibilities have been examined, can cladistic implications be explored.

APPENDIX 10.1

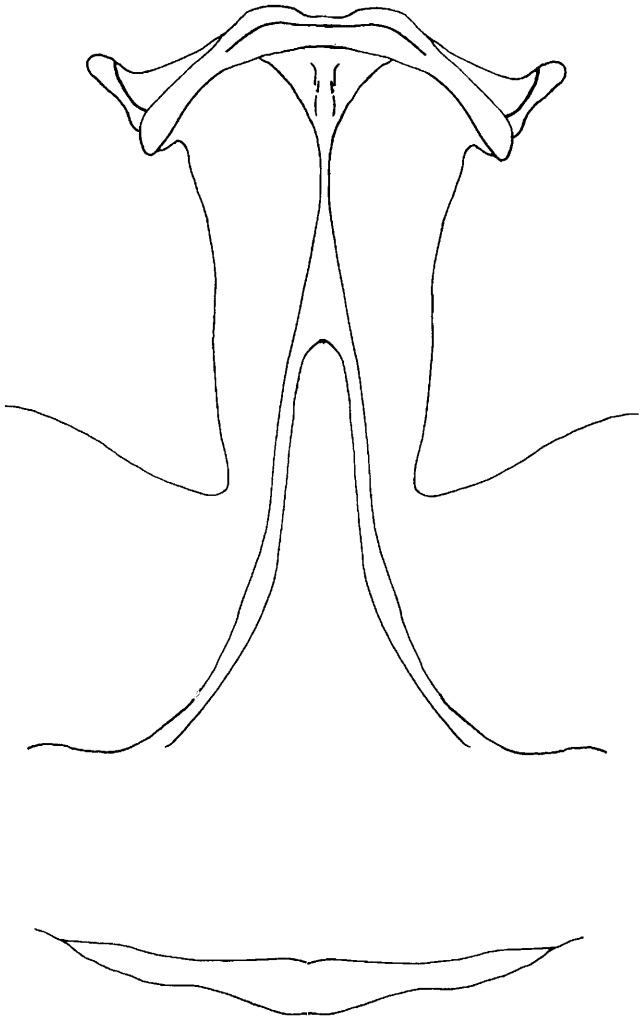


Fig. 1

Fig. 1 Dorsal view of the metendosternite of *Orgyges marculasea* (Passalidae).

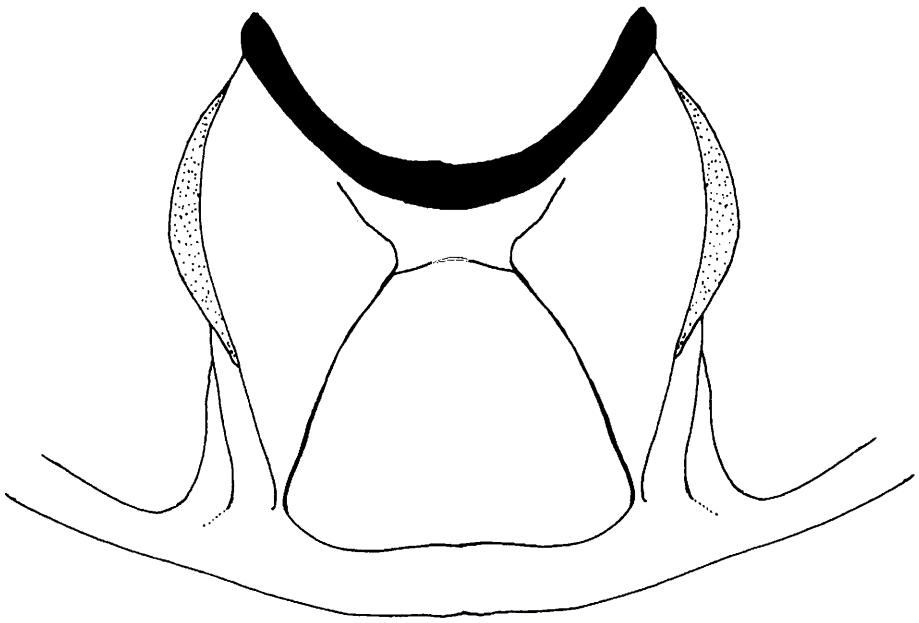


Fig. 2

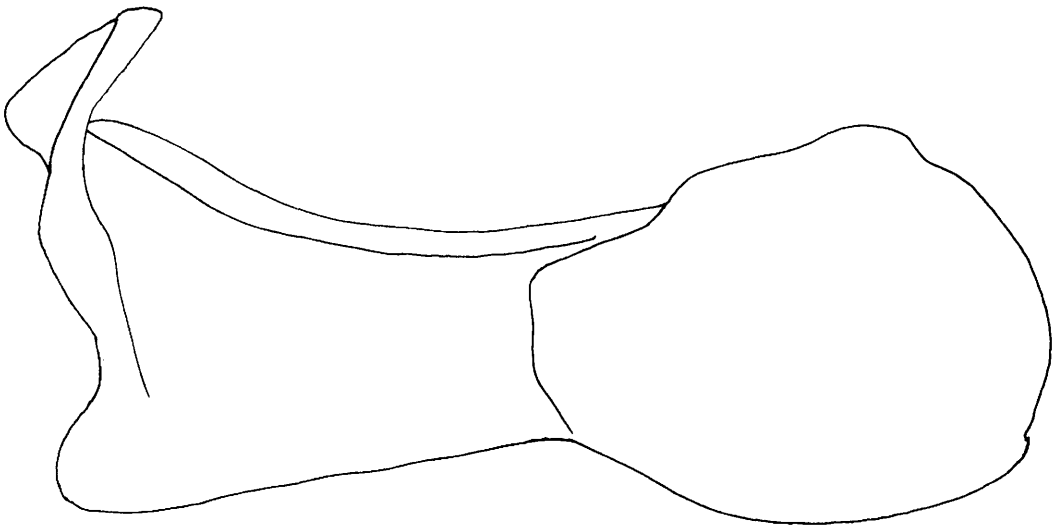


Fig. 3

Fig. 2 Frontal view of the metendosternite of *Orgyges marculasea* (Passalidae).

Fig. 3 Lateral view of the metendosternite of *Orgyges marculasea* (Passalidae).

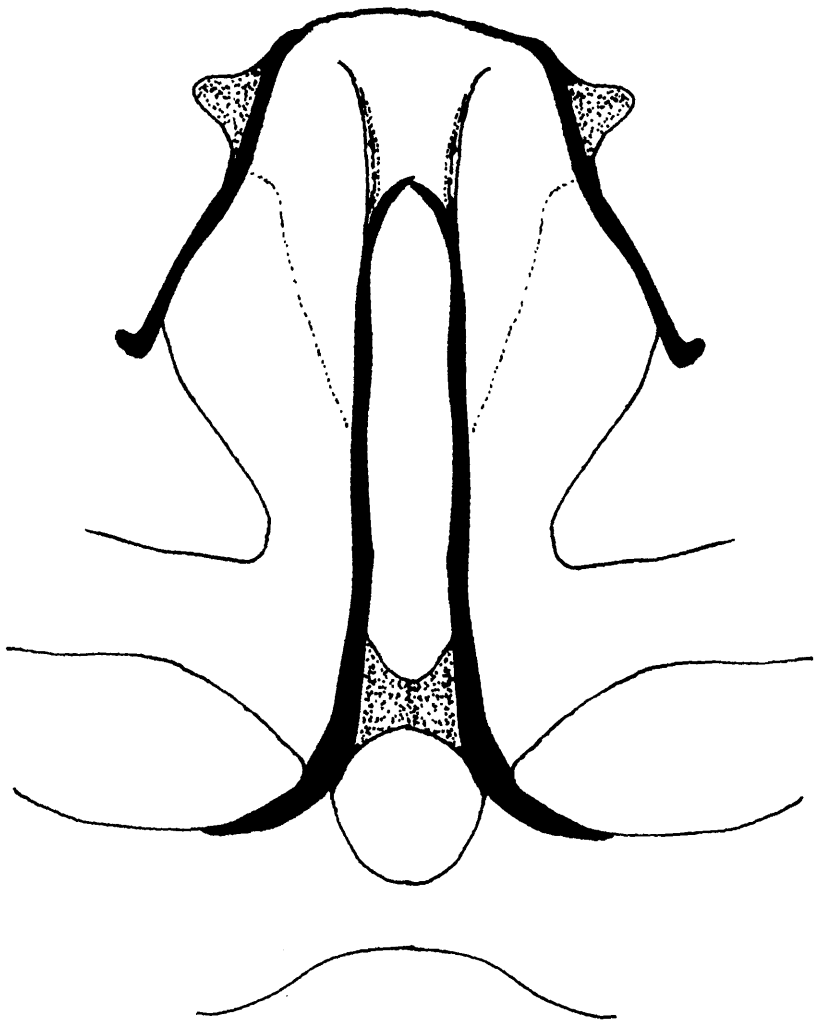


Fig. 4

Fig. 4 Dorsal view of the metendosternite of *Passalus punctiger* (Passalidae).

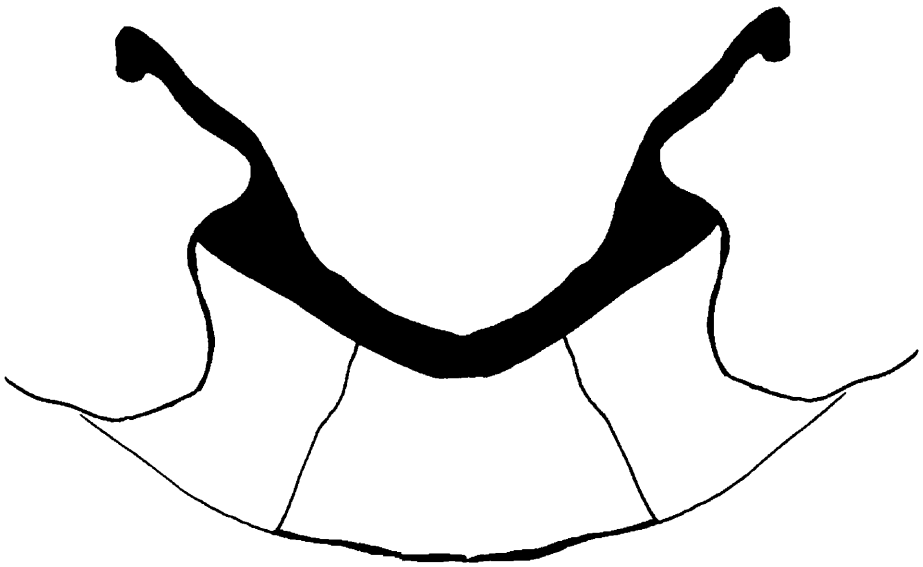


Fig. 5

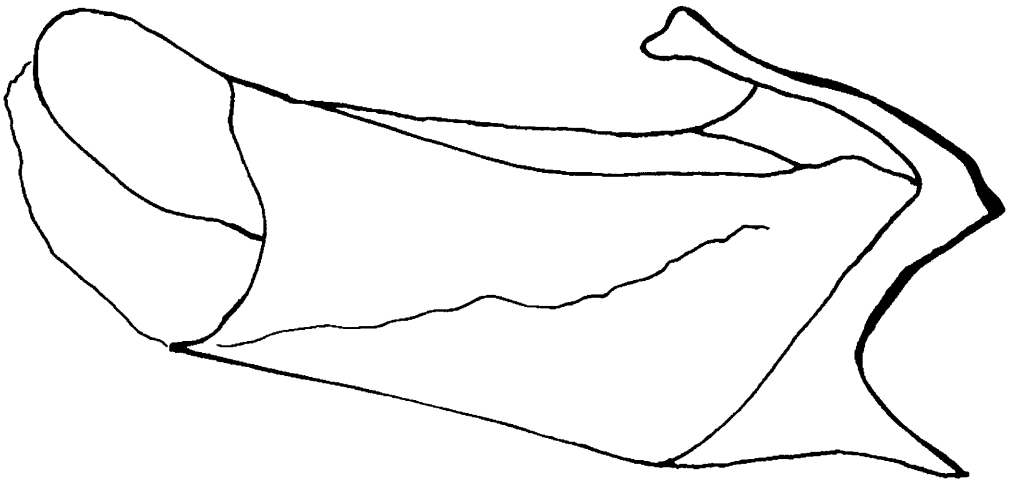


Fig. 6

Fig. 5 Frontal view of the metendosternite of *Passalus punctiger* (Passalidae).

Fig. 6 Lateral view of the metendosternite of *Passalus punctiger* (Passalidae).

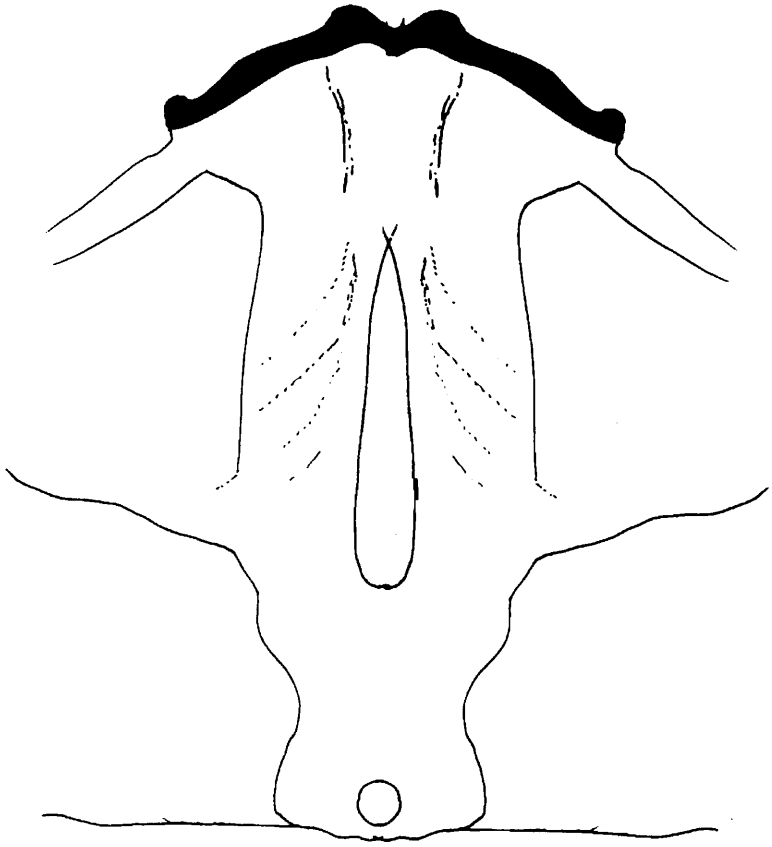


Fig. 7

Fig. 7 Dorsal view of the metendosternite of *Odontotaeinius zodiacus* (Passalidae).

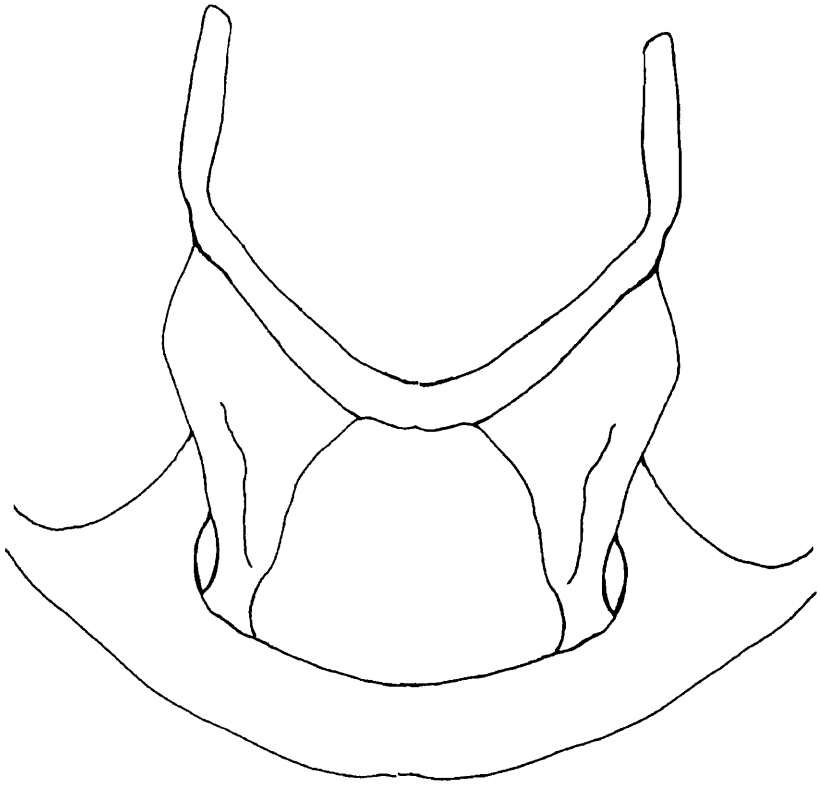


Fig. 8

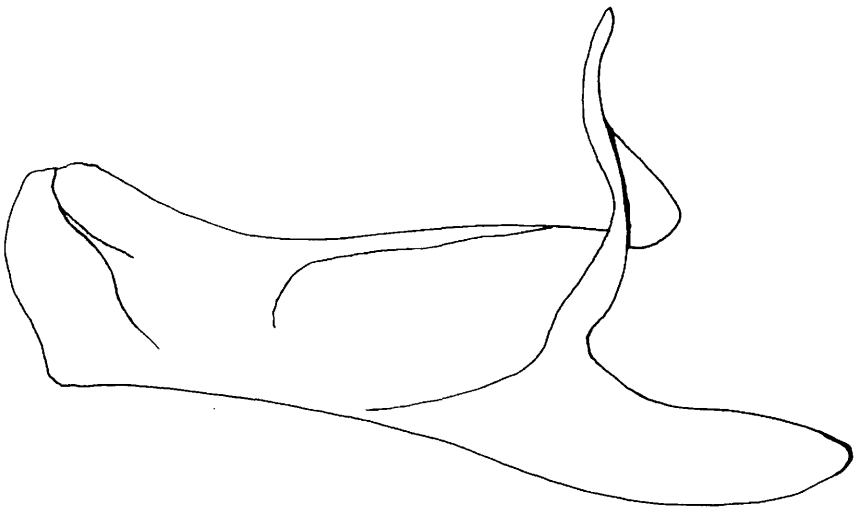


Fig. 9

Fig. 8 Frontal view of the metendosternite of *Odontotaeinius zodiacus* (Passalidae).

Fig.9 Lateral view of the metendosternite of *Odontotaeinius zodiacus* (Passalidae).

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