

SECONDARY SEXUAL FEATURES IN BEETLES
AND THEIR ROLE IN SPECIFIC MATE RECOGNITION

by

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ABSTRACT

The variety, siting and function of male secondary sexual features in the Staphylinidae are examined. Emphasis is placed on features which are thought to function in specific mate recognition, particularly in the Staphylininae where closely related species frequently occur syntopically. In 116 genera belonging to tribes of the Staphylinidae, the secondary sexual and genital characters are systematically tabulated and discussed, identifying those character states which may be primitive. This acts as a preface for an investigation into a monophyletic group of species, the Philonthus sordidus-Group, using an average linkage cluster analysis to establish a basis from which phylogenetic relationships may be assessed in species in which morphological, behavioural and ecological studies are also undertaken.

Intraspecific variation in secondary sexual and other external characters is demonstrated morphometrically, using the coefficient of variation, in Quedius mesomelinus and related geographical races and species which are sympatric over part of their range. Genital and secondary sexual characters are shown to be less variable than other external characters. The range of variation within the area of overlap is compared with that beyond.

The structure of staphylinine male genitalia is described, detailing the distribution and function of peg-like setae situated on the lateral lobe. Dissections of pairs of beetles in copula show the position of the genitalia during mating. Mating behaviour in a number of staphylinid species is described with the aid of time lapse photography, and mating behaviour in the Coleoptera as a whole is reviewed from the literature and accompanied by information concerning the operation of reproductive isolating barriers. Comparative and quantitative studies of intra and inter-specific mating behaviour in closely related species of Philonthus are presented.

LIST OF CONTENTS

ABSTRACT

SECTION 1	<u>GENERAL INTRODUCTION</u>	1
SECTION 2	<u>MATERIALS AND METHODS</u>	19
2.1	COLLECTION OF SPECIMENS	"
2.2	REARING AND CULTURING	"
2.3	SCANNING ELECTRON MICROSCOPY	20
2.4	TRANSMISSION ELECTRON MICROSCOPY	21
2.5	PHOTOGRAPHY	"
2.6	HISTOLOGY	"
2.7	DRAWINGS	22
2.8	DISSECTION AND STORAGE OF MATERIAL	"
SECTION 3	<u>THE STRUCTURE OF THE GENITALIA</u>	23
3.1	STAPHYLINIDAE	"
3.2	STAPHYLININI	"
3.3	MUSCULATURE ASSOCIATED WITH THE GENITALIA	24
3.4	STRUCTURE AND FUNCTION OF PEG SETAE	30
SECTION 4	<u>SURVEY OF SECONDARY SEXUAL FEATURES IN THE STAPHYLINIDAE</u>	36
	INTRODUCTION	"
4.1	CLASSIFICATION OF SECONDARY SEXUAL STRUCTURES	"
1.	<u>Structures involved in division of labour</u>	"
2.	<u>Structures which play a "mechanical role in mating</u>	37
3.	<u>Structures which play a role in sensory reception during mating</u>	38
4.	<u>Structures which play a role in specific mate recognition</u>	"
a)	<u>Intra-sexual Selection</u>	"
b)	<u>Intra-specific epigamic selection</u>	"
1.	production of non-tactile signals	"
2.	production of tactile signals	"
i)	from a non-specific structure	39
ii)	from a specific structure	"
4.2	CLASSIFICATION, BY SITING, OF THE SECONDARY SEXUAL CHARACTERS IN THE STAPHYLINIDAE	42
4.2.1	<u>Head</u>	"
4.2.2	<u>Thorax</u>	43
4.2.3	<u>Abdomen</u>	47
1.	<u>Ventral Features</u>	"
a)	<u>Emargination and lobing of sclerites</u>	"
b)	<u>Occurrence of patches of pubescence and bundles of setae</u>	51
c)	<u>Occurrence of patches of peg setae</u>	53
d)	<u>Occurrence of combs of robust setae</u>	"
e)	<u>Elaborate development of abdominal sternites (i.e. angled projections, knobs, prongs)</u>	"
f)	<u>Extravagant development of the apical segments</u>	54

2.	<u>Dorsal Features</u>	54
4.2.4	<u>Genitalia</u>	55
4.3	<u>Examination of closely related species</u>	
	<u>pairs/groups</u>	64
4.3.1	<u>Proteininae</u>	65
4.3.2	<u>Omaliinae</u>	74
4.3.3	<u>Oxytelinae</u>	79
4.3.4	<u>Paederinae</u>	88
4.3.5	<u>Staphylininae</u>	99
4.3.6	<u>Tachyporinae</u>	170
4.3.7	<u>Aleocharinae</u>	197
4.3.8	<u>Pselaphidae</u>	204
SECTION 5	<u>MATING BEHAVIOUR</u>	215
	<u>INTRODUCTION</u>	"
5.1	<u>Methods for Observation of Mating Behaviour</u>	"
5.2	<u>List of Species in which Mating Behaviour</u>	
	<u>Observed</u>	216
5.2.1	<u>Philonthus cephalotes, P. parvus, and P. sordidus</u>	217
5.2.2	<u>Philonthus discoideus</u>	239
5.2.3	<u>Philonthus fimetarius</u>	240
5.2.4	<u>Philonthus longicornis</u>	"
5.2.5	<u>Philonthus marginatus</u>	241
5.2.6	<u>Philonthus politus</u>	242
5.2.7	<u>Philonthus tenuicornis</u>	244
5.2.8	<u>Quedius mesomelinus</u>	"
5.2.9	<u>Quedius tristis</u>	248
5.2.10	<u>Rugilus orbiculatus</u>	249
5.2.11	<u>Othius myrmecophilus</u>	"
5.2.12	<u>Gyrophymus fracticornis</u>	251
5.2.13	<u>Oxytelus sculptus</u>	253
5.2.14	<u>Tachinus signatus</u>	254
5.2.15	<u>Cypha longicornis</u>	"
5.3	<u>Intra and inter-specific behaviour in</u> <u>Philonthus cephalotes and P. sordidus</u>	256
5.3.1	<u>General Observations</u>	259
5.3.2	<u>Further Observations of Interspecific</u> <u>Behaviour in Philonthus species</u>	270
5.4	<u>Effect of Antennectomy in male Philonthus</u> <u>sordidus</u>	272
5.4.1	<u>Reaction of antennectomised and normal male</u> <u>Philonthus sordidus to freshly crushed females</u>	275
5.4.2	<u>Pairs in copula</u>	276
5.5	<u>Mating Behaviour Review</u>	283
5.5.1	<u>SYSTEMATIC INDEX OF SPECIES FOR WHICH</u> <u>INFORMATION ON MATING BEHAVIOUR IS AVAILABLE</u>	284

5.5.2.1	<u>CARABIDAE</u>	307
2	<u>HALIPLIDAE</u>	311
3	<u>DYTISCIDAE</u>	"
4	<u>GYRINIDAE</u>	312
5	<u>SILPHIDAE</u>	313
6	<u>STAPHYLINIDAE</u>	"
7	<u>HYDROPHILIDAE</u>	320
8	<u>HISTERIDAE</u>	321
9	<u>HELODIDAE</u>	322
10	<u>LUCANIDAE</u>	"
11	<u>PASSALIDAE</u>	324
12	<u>SCARABAEIDAE</u>	325
13	<u>EUPRESTIDAE</u>	331
14	<u>ELATERIDAE</u>	333
15	<u>EUCNEMIDAE</u>	334
16	<u>LYCIDAE</u>	"
17	<u>DRILIDAE</u>	"
18	<u>PHENGODIDAE</u>	"
19	<u>LAMPYRIDAE</u>	"
20	<u>CANTHARIDAE</u> (original observations)	336
21	<u>DERODONTIDAE</u>	343
22	<u>DERMESTIDAE</u>	"
23	<u>BOSTRICHIDAE</u>	345
24	<u>ANOBIIDAE</u>	"
25	<u>PTINIDAE</u>	346
26	<u>CLERIDAE</u>	"
27	<u>MELYRIDAE</u>	347
28	<u>CUCUJIDAE</u>	349
29	<u>CRYPTOPHAGIDAE</u>	350
30	<u>COCCINELLIDAE</u>	"
31	<u>RHIPIPHORIDAE</u>	352
32	<u>TENEBRIONIDAE</u>	353
33	<u>MELOIDAE</u>	356
34	<u>CERAMBYCIDAE</u>	361
35	<u>BRUCHIDAE</u>	364
36	<u>CHRYSOMELIDAE</u>	"
37	<u>ATTELABIDAE</u>	366
38	<u>SCOLYTIDAE</u>	"
39	<u>BRENTHIDAE</u>	369
40	<u>RHYNCOPHORIDAE</u>	370
41	<u>CURCULIONIDAE</u>	"
42	<u>Mating Behaviour Review Discussion</u>	374
5.6	<u>Cross Mating and Hybridisation</u>	379
SECTION 6	<u>VARIATION IN MORPHOLOGICAL CHARACTERS OF TWO "PARTIALLY" SYMPATRIC SPECIES, WITH PARTICULAR REFERENCE TO THE MALE GENITALIA IN DIFFERENT GEOGRAPHICAL LOCATIONS</u>	384
6.1	<u>INTRODUCTION</u>	"
6.2	<u>Materials and Methods</u>	391
6.3	<u>Results</u>	396
6.4	<u>Discussion of Results</u>	398
6.4.1	<u>Comparison of the variation, measured by the coefficient of variation in each character</u>	"

6.4.2	<u>Comparison of means and ranges for each character</u>	405
6.4.3	<u>Comparison of species using bivariate plots</u>	415
6.4.4	<u>Geographical trend in median lobe length</u>	426
6.4.5	<u>Correlation between median lobe length and pronotum length</u>	429
6.5	<u>Falkland Island <i>Q. mesomelinus</i></u>	"
6.6	<u>Shetland Island <i>Q. mesomelinus</i></u>	430
6.7	<u>Peg Patterns</u>	431
6.8	<u>Proposed status of <i>Q. maurus</i>; <i>Q. mesomelinus</i> and its "varieties"</u>	434
6.9	<u>Summary</u>	439
SECTION 7	<u>PHYLOGENETIC RELATIONSHIPS IN THE <i>Philonthus sordidus</i>-Group</u>	440
7.1	<u>Staphylininae</u>	"
7.1.1	<u>Platyprosopini</u>	"
7.1.2	<u>Diochini</u>	442
7.1.3	<u>Othiini</u>	"
7.1.4	<u>Xantholinini</u>	443
7.1.5	<u>Staphylinini</u>	"
7.1.5.1	<u>Xanthopygina</u>	444
7.1.5.2	<u>Staphylinina</u>	448
7.1.5.3	<u>Philonthina</u>	451
7.1.5.4	<u>Quediina</u>	454
7.1.5.5	<u>Amblyopinina</u>	455
7.1.5.6	<u>Holisina</u>	"
7.1.6	<u>Polarity of character states relating to male Staphylinini genitalia and secondary sexual characters</u>	"
7.2	<u><i>Philonthus-sordidus</i>-Group</u>	460
7.2.1	<u>Characteristics of the <i>P. sordidus</i> Group</u>	471
7.2.1.1	<u>Chaetotaxy</u>	472
7.2.1.2	<u>Microsculpture</u>	474
7.2.2	<u>Characters used to separate species in the <i>P. sordidus</i>-Group</u>	477
7.2.3	<u>Numerical Taxonomy</u>	478
7.2.3.1	<u>Coding of Characters</u>	485
7.2.3.2	<u>Results of Numerical Taxonomy</u>	490
7.2.4	<u>Suggestions Regarding Possible Relationships within the <i>P. sordidus</i>-Group</u>	495
7.2.5	<u>Possible Relationships of Species excluded from the <i>P. sordidus</i>-Group</u>	497
SECTION 8	DISCUSSION	499
	REFERENCES	503
	ACKNOWLEDGEMENTS	532
	APPENDIX 1. List of species in which cross mating and hybridisation has occurred.	533
	APPENDIX 2. Raw and summarised data from <u><i>Quedius mesomelinus</i></u> and related species.	541

SECTION 1

GENERAL INTRODUCTION

The role of secondary sexual features in specific mate recognition is a topic which has not been considered in detail in the Insects. In the family Staphylinidae (Coleoptera), there is a wealth of morphological features to which this function could be attributed. However, although these features have been frequently studied in the past, their function seems to have been entirely overlooked although they have been extensively used as taxonomic characters for classification. In order to introduce this topic it is necessary firstly, to summarise the current thinking on the modes of animal speciation and the development of reproductive barriers, and secondly, discuss recognition in connection with mate selection and the function of secondary sexual features.

An essential pre-condition for the occurrence of evolution in any population is the existence of heritable variation upon which natural selection, or other agencies, can act (Darwin, 1859, and other more recent workers). Sexual reproduction is a mechanism whereby variation can be introduced into a genetic line and this is employed by the great majority of living organisms. In this way, continuing genetic variation may be provided which would buffer a species for unfavourable changes by giving greater adaptability and thus chance of survival.

Multiplication of species can occur through several possible modes and these will be briefly discussed under three main categories. Firstly, instantaneous speciation is the production of a single individual that is reproductively isolated from the species to which the parental stock belongs. This individual is then reproductively

and ecologically capable of establishing a new species (Mayr, 1963).

Secondly, speciation through major chromosomal changes has been considered to occur by polyploidy. In sexually reproducing animals this is rare, all the proven cases occur in those species which reproduce either by permanent parthenogenesis, self fertilising hermaphroditism, or by hybridisation of genetically and taxonomically different individuals. This type of speciation requires that the population of hybrids is segregated until reproductive isolation is acquired, to prevent swamping by the parental populations. The evolutionary importance of hybridisation is considered to be small in the majority of animals since when fertile hybrids are produced genetic imbalance often results in their lowered fitness. Evidence has been collected from the literature of hybridisation in the Coleoptera, to provide information on its frequency and the reasons for its occurrence. The breakdown of reproductive barriers are of particular interest, especially those which are thought to be involved in specific mate recognition. There is no evidence to suggest that hybridisation occurs in groups where distinctive specific recognition signals are known to be employed, at close quarters, during courtship. Where hybridisation does occur, it is in groups which generally achieve reproductive separation by difference in mating times, host specificity or habitat differences. These phenomena are termed "mate avoidance" by Hammond (in press^a; refer to Section 5.6 and Appendix 1).

Thirdly, speciation by gradual divergence concerns populations. A single population may split and diverge allowing separate species to develop. Mayr (1963) recognises two types of gradual divergence, that involving geographical separation (allopatric speciation) and speciation without geographical separation (sympatric speciation). An alternative consideration, which does not rely on the geographical setting in which speciation takes place, looks at the process in terms of gene flow, i.e. speciation in isolation and speciation in

the face of gene flow. In sexually reproducing animals one way in which a new species develops is when a population (which is geographically isolated from its parental stock) acquires characters during this period of isolation which promote or guarantee reproductive isolation if the external barriers break down (Mayr, 1963). Cain (1971) regards spatial isolation as being a necessary pre-condition for sufficient divergence to take place. He points out that there are several reasons why isolated populations will diverge genetically and suggests that a better knowledge of geographical variation would show that much of it is adaptive or is correlated with adaptive features. Such variation probably affects all the characters of an organism, and not only the most obvious adaptations and specialisations. Some characters may therefore be the necessary consequence of the same process and their distribution will also be determined by selection. Local selection will therefore produce genetical and ecological divergence of populations. If such populations were to meet and overlap, this would be a basis from which they could develop efficient reproductive barriers to remain genetically separated, with ecological specialisations to reduce competition and promote ecological compatibility.

Sympatric and parapatric speciation may or may not occur in the face of gene flow. Mayr (1963) defines sympatric speciation as " a) the establishment of new populations of species in different ecological niches within the normal cruising range of the individuals of the parental populations, and b) the reproductive isolation of the founders of the new population from individuals of the parental population, gene flow being prevented by intrinsic factors". Cain (1971) regards regional differentiation, leading to specific status in the face of gene flow, as semisympatric speciation since it involves ecological allopatry and genetical contiguity and considers it to be unlikely. Bush (1975) believes that sympatric speciation is largely

limited to phytophagous and zoophagous parasites and parasitoids. As these represent a large proportion of the insects the mechanism may be relatively common. Speciation is considered to occur through host changes and chromosome rearrangements are rarely involved. Other sympatric patterns of divergence involve temporal, chemical (pheromone) and symbiotic factors, hybridisation and polyploidy. The latter two, whilst of major importance in plant speciation, play an insignificant role in animal speciation.

Thoday & Boam (1959) consider the possibility that two components of a population can diverge without any isolation limiting gene flow between them. Disruptive selection and genetic diversity in a population can be favoured by heterogeneity of environmental conditions. Their theory is illustrated with evidence from populations of Drosophila, which were experimentally exposed to disruptive selection and assortative mating. It has been shown mathematically by Maynard Smith (1966), that the establishment of a stable polymorphism in a heterogeneous environment may lead to isolation by habitat selection. He regards this as a crucial step in sympatric speciation. This is confirmed by Dickinson & Antonovics (1973) in their theoretical considerations of sympatric divergence. They suggest that it is possible to establish a polymorphism, both for a single gene and a polygenic character, if there is the capacity for more than one niche in a habitat. This can occur over a wide range of conditions and reproductive isolation can arise in response to the deleterious effects of gene flow, and assortative mating. Thus, heterogeneity of the environment can have far reaching effects on the genetic architecture of the population.

Huettel & Bush (1972) have studied the genetics of host selection and its bearing on sympatric speciation. They suggest that an insect is conditioned to prefer a particular host for feeding

and reproduction. Nevertheless, there is no conclusive evidence that conditioning is strong enough to produce isolation sufficient for genetic divergence and speciation. Where mating takes place on the host and if it is assumed that host selection is genetically controlled, then a minor change in the locus associated with host selection could drastically alter the site of mating and thus mate selection. For example, in Procecidochares (Diptera: Tephritidae) there is evidence that major differences in host selection between two sibling species are controlled by two alleles at a single locus, the expression of which is strongly influenced by conditioning. Similar evidence has also been obtained for blue and coal tits, and Rhagoletes fruit flies (Partridge, 1979).

Parapatric speciation may occur whenever species evolve as contiguous populations in a continuous cline (Bush, 1975). Murray (1972) considers that significant differentiation can take place in the face of massive gene flow, provided firstly, that the conditions of strong selection and independent regulation of population size are met, and secondly, that it is likely that the architecture of the genetic system may reinforce and enhance the differentiation of coadapted gene complexes. Parapatric speciation resembles speciation by the Founder Effect (see Bush, 1975) which is the establishment of a new population by a few original founders which carry only a small fraction of the total genetic variations of the parental population (Mayr, 1963). According to Bush (1975) parapatric speciation differs in three major ways; firstly, no spatial isolation is required, secondly, the level of vagility in animals undergoing parapatric speciation is exceptionally low, and thirdly, reproductive isolation arises simultaneously with the penetration and exploitation of a new habitat by genetically unique individuals.

The development and improvement of reproductive barriers to

maintain the isolation of incipient species is known as the Wallace Effect. Hybrids produced, in cases where allopatric populations subsequently become sympatric, are at a disadvantage owing to a reduced fitness, because of the increased adaptiveness of the homozygotes of both populations. There will therefore be selection operating against heterogametic matings, favouring the development of reproductive barriers. Pat~~ter~~son (1978) does not accept the concept of reinforcement of reproductive barriers, where sympatric species overlap, because he considers that the barriers are primarily concerned with recognition, to ensure assortative mating so that the advantageous biparental genes are effectively represented in the next generation. Isolation is only a secondary effect and he prefers to refer to the barriers as specific mate recognition systems. Evidence for the Wallace Effect can be sought from several sources. These include, artificial selection experiments for assortative mating, examination of hybrid zones for changes in frequency of hybridisation, studies of pairs of species which are sympatric in some areas but allopatric in others (with a comparison of the strength of isolation in the two cases), and comparisons between groups of species having some sympatric and some allopatric representatives. Murray (1975) points out that the soundest body of evidence for the Wallace Effect is the comparison of allopatric and sympatric species. The null hypothesis is that allopatric pairs are more reproductively isolated due to the greater potential for differentiation in isolation, e.g. ecological diversity. Evidence to the contrary is a good indication that the Wallace Effect is in operation.

Reproductive barriers have been classified by Mayr (1963) as the biological properties of individuals that prevent the interbreeding of populations that are actually, or potentially, sympatric. These

can be grouped into two categories of premating and postmating barriers:

Terminology of:-

Mayr (1963)

Hammond (in press^b)

Premating Barriers

seasonal and habitat isolation	mate avoidance
ethological isolation (visual, auditory and chemical stimuli)	mate rejection
mechanical isolation	mate incompatibility

Postmating Barriers

gametic mortality
zygote mortality
hybrid inferiority
hybrid sterility

The gradual development and improvement of reproductive barriers, or the Wallace Effect, must be distinguished from character displacement. In this context this is considered to be the result of competition for resources in already reproductively isolated populations, to enable ecological compatibility. The Wallace Effect, on the other hand, is a stage in the process of speciation.

Bush (1975) has considered the development of reproductive barriers in the different modes of speciation. Premating barriers, where they develop, are usually improved first in the zone of contact, so that hybrids eventually become rare or absent. This can occur very rapidly, or occasionally a more or less permanent narrow hybrid belt may be established. Speciation in isolation may be initiated by either, subdivision or the breakaway of a founder population. In the subdivision of a population, postmating reproductive barriers are a fortuitous result of long term adaptive

genetic changes during isolation. Speciation by a founder population is similar to subdivision, in that incipient reproductive isolation arises by chance after the founders have established themselves in a new territory. Chromosome rearrangements are thought to be frequently involved and thus postmating reproductive isolation may occur. In both cases there is, however, no direct selection for intrinsic barriers to gene flow, since hybrids are not produced between the parent and daughter populations. Only if the sister populations re-establish contact will there be improvement of postmating and selection for premating barriers, and this will be limited to the hybrid or overlap zone.

In parapatric speciation, chromosome rearrangements may be involved in the initiation of speciation and postmating and premating barriers arise as individuals penetrate a new habitat. Selection favours the evolution of reproductive isolation because hybrids in the overlap areas are of reduced fitness.

For sympatric speciation to occur, premating barriers must arise before a population shifts to a new niche. Chromosome rearrangements are thought to be rarely involved while host changes often occur. Mate selection often depends on host selection, where the principal reproductive barriers are ecological (of the mate avoidance type) and postmating barriers do not appear to be involved.

Reproductive barriers may involve specific signals concerned with mate recognition. The selection of a mate is vitally important and it is common to ascribe to sexual behaviour the role of a specific signal system. This enables the males and females to check one another's identity before they mate (Manning, 1966). Secondary sexual structures may be involved. In beetles these are particularly evident in males and may have a number of functions, including division of labour, sexual selection, a mechanical or

sensory role in mating, part of an attractant device or recognition device. These will be discussed in detail in Section 4. Recognition devices need not be structural, and throughout the Insecta many different types are displayed:-

<u>structural</u>	<u>non-structural</u>
visual	visual (behavioural)
tactile	tactile (behavioural)
	chemical (olfactory, contact chemoreception)
	acoustic
	non-specific form (behavioural)

Some examples from the major Orders will be discussed.

Odonata

Watson (1966) and Paulson (1974) postulate mechanical isolation at two possible points; in the tandem position and the copulatory position. The genital structures provide a "lock and key" type of mechanism. Corbet (1962) mentions that amongst the Anisoptera, it is only in Aeshnidae that the prothorax and head of the female actually fit the male superior appendages as interlocking devices. This is thought to be a releaser for the initial stages of courtship. Visual recognition is based on female colouration (Paulson, 1974), size of the female body, colour and transparency of wings in European species of Calopteryx; female head and thorax, and transparent wings in Epallage fatime; movement in Platycnemis dealbata; and a distal pale spot on the abdomen of Ischnura elegans. These features act as releasers for courtship behaviour (Corbet, 1962). The flight stroke of the female may also be a recognition factor. Visual recognition can be regarded as the first of several factors which help to achieve reproductive isolation. An example of tactile stimulation,

of the female, is given for Platycnemis (Paulson, 1974). The male has expanded tibiae which are used for this purpose.

Mixed pairs of species have been known to mate. These belong mainly to the genera, Aeshna, Anax, Dromogomphus, Styluria, Tetragoneuria and Sympetrum (Neville, 1959; and Corbet, 1962). In these cases reproductive isolation is not achieved by mechanical means.

Orthoptera

The males of many of the Orthoptera stridulate to produce characteristic songs. Sound production is discussed by Ragge (1965). In the Tettigoniidae (bush crickets), Gryllidae (true crickets) and Gryllotalpidae (mole crickets), sound production is confined to the males and is alary. Representatives of the Gryllidae have a special courtship song which is more subdued than the normal song. In the Acrididae (grasshoppers), only the males have a fully developed stridulatory apparatus, although a vestigial apparatus may be present in the female. Such females may stridulate with a song, similar to that of the male, but which is not so loud. The females usually only sing in response to the male courtship song. Stridulation in grasshoppers is femoro-alary. Body swaying and movement of the head and palps may accompany stridulation in the male courtship display.

Information is carried in the song in different ways. The song of two related species may differ in their carrier frequency, pulse period and pulse length, and the way in which brief pulses are connected together to form syllables or chirps. The song pattern may form an important inter-specific barrier. From studies on closely related species it has been found that the song carrier frequency varies between individuals by only a few percent, but between species by an octave. The pulse interval varies as much within the songs of the individuals as does the mean interval within the species, but there may be little or no overlap with closely related species (Bennet-Clark, 1975).

Ragge (pers. comm.) suggests that true sympatric pairs of species, with slight morphological differences, do not really occur in Britain but do so in Europe. Here, they have subtle ecological differences but can be found together. Chorthippus biguttulus and C.mollis are sympatric in Europe. These two species have great differences in song and this is the sole recognition device. If under experimental conditions singing is prevented, they will interbreed and produce fertile hybrids which have an intermediate song. Chorthippus dorsatus and C.dichrous are also sympatric in Europe with distinctive songs and have a visual element in recognition as well. The male performs stereotyped movements during courtship. Similarly, some males, which possess clubbed antennae, wave them, along with the palps, in part of a complex pattern of behaviour. In some tropical grasshoppers there is no stridulation and recognition is thought to be entirely visual.

Dictyoptera

Blattaria (cockroaches)

Some cockroaches produce sound, but it is doubtful whether this is ever used for mate recognition. Stridulation in males during courtship has so far been observed in Nauphoeta cinerea. Various behavioural patterns of males of different Blaberids suggest that vibratory and pumping movements, possibly employed to disseminate a pheromone, lead to the production of rhythmical sounds, in N.cinerea, which may be involved in sexual recognition (Roth & Hartman, 1967). Mate recognition is usually achieved using pheromones. The male commonly has a gland, situated on the seventh abdominal tergite, on which the female appears to feed. In Blattella germanica, although recognition appears to be mediated through contact chemoreception, the male must make antennal contact with the female before courtship is initiated. In Periplaneta americana and Byrsotria fumigata, the

female produces a volatile sex attractant (Roth & Willis, 1968).

Olfactory and tactile stimuli are principally responsible for releasing various patterns of behaviour during courtship and mating in most cockroach species (Roth, 1965). Different species may interbreed if confined together (Roth, 1970). Reproductive isolation involves differences in behaviour or sexual behaviour releasing stimuli, but it is apparent that both sexes of several species of the genus Blaberus may respond to one another's pheromones. However, any eggs produced between them are generally infertile.

Mantodea (praying mantids)

The first phase of recognition in the praying mantids, is the visual recognition of the female by the male (Roeder, 1935). If a receptive male and female are placed together, the movements of one will eventually be detected by the other. If the female sees the male first, he will be watched or approached and may be eaten. The male, however, has better vision and generally sees the female first, watches her and freezes. After several hours the male takes some imperceptible steps in the direction of the female. When the male finally comes near, he vibrates his wings rapidly and jumps onto the female dorsum. The female shows no sign that she recognises the presence of the male. If the male is detected during his approach phase, he will be attacked and eaten, head first, to destroy the inhibitory centre in the suboesophageal ganglion. The effect of this is to bring the male into the mating position, whereupon copulation is immediately achieved.

Hemiptera

Acoustic behaviour in the Hemiptera is reviewed by Leston & Pringle (in Busnel, 1964). Sound production is used for two purposes, the first for warning or defence, the calls here having

no regularity, and the second for mating, courtship and aggregation, the calls here being more regular.

In the Homoptera, stridulation has been recorded in the Auchenorrhyncha and isolated cases in the Sternorrhyncha. Stridulation is also recorded from the Heteroptera, where in some species both sexes call while in others only males call. The common song changes abruptly to the courtship call at a distance of about 1 cm from a female, and if the female escapes without copulating the common song recommences. This phenomenon has been noted in the Corixidae, Notonectidae, Cydnidae, Pentatomidae, and Piesmididae. In the pentatomid, Carpocoris pudicus, there is a female call in addition to the two usual male songs. This may possibly be an acceptance song which releases male copulatory behaviour. Studies of closely allied species suggest that the courtship song acts as a barrier to cross mating.

Diptera

Downes (1969, 1978) reviews swarming behaviour in the Diptera. In the most primitive families, mating takes place in flight at a visually determined assembly station which is occupied by both sexes. The female is recognised visually by her movement, the males often having highly specialised eyes. In most of the Culicidae recognition is by a highly specialised auditory system mediated by plumose antennae. Specificity of mating is thought to be achieved by the specificity of the assembly station, since the visual or auditory response to the female is not adequately specific. It remains uncertain whether there is any contact recognition.

In the Nematocera, mating in flight is rare and species specific courtship, or epigamic, displays are frequently utilised.

Drosophila melanogaster produces a series of low frequency pulses

from intermittent wing beats. Different species have been shown to produce different songs. The females receive the sound by feathery aristae on the antennae (Bennet-Clark, 1975; and Ewing, 1978). Cloudsley-Thompson (1976) states that the visual components of the male displays of Drosophila spp. are not a means by which a female recognises a mate, but recognition usually occurs at the onset of courtship when the male taps the female with his fore legs.

In other species, including members of the Tipulidae, pheromones may be used to attract females from a distance. It is unlikely that these are species specific.

Hymenoptera

In many parasitic Hymenoptera copulation is preceded by elaborate courtship displays which include species specific characteristics. These are the movements of the male, elements of which are repeated until the female exhibits receptivity. Such elements include, movements of the wings, legs, antennae and mouth parts. The wing movements produce vibrations which are perceived both as sounds and as tactile stimuli through the male legs. Pheromones may also be involved (Miller & Tsao, 1974; and Assem, 1975).

Lepidoptera

Communication in the Lepidoptera is extensively reviewed by Silberglied (1977). Courtship follows a basic pattern throughout the Lepidoptera, where males are attracted to females by long distance communication, either visually (many butterflies) or chemically (many moths). Short distance communication and close approach is mediated by female pheromones. This is followed by stereotyped behaviour on the part of the male which includes, disseminating aphrodisiacs and/or the presentation of visual, auditory of tactile signals which inhibit the locomotion of receptive females.

Visual stimuli are involved in the approaches and courtship behaviour, these include female colour, ultraviolet reflection patterns, movement and size. Males may initially be indiscriminate but usually distinguish females on the basis of colour, odour, or both. Among sexually dimorphic species colour plays an important role, however this may be a problem among butterflies with seasonal forms and polymorphism. Courtship in all Lepidoptera involves pheromones at some stage.

In moths, the females initiate courtship and cues are generally olfactory. They release sex pheromones which elicit a hierarchy of responses in males. Orientation may involve anemotaxis, chemical cues, sound and vision; however, visual cues are not necessary. Different compounds or a single compound may serve to attract and excite males. Males may release highly volatile aphrodisiac pheromones to inhibit female locomotion.

The stereotyped species specific behaviour patterns serve also as reproductive barriers between closely related species. Prezygotic barriers are thought to be of greater importance than genetic incompatibility or sterility. In some cases mechanical barriers are operative although Guillaumin (1974) suggests that too much emphasis is placed on the diverse genitalic differences between males. Likewise Silberglied (1977) considers that physical or mechanical ("lock and key") barriers are not of importance. The major prezygotic barriers, temporal, ecological and ethological (including specific visual and chemical cues) combine to isolate sympatric populations of different species.

In the French and Spanish butterfly fauna, 24 different natural hybridisations are known (Guillaumin, 1974); however, Silberglied (1977) notes that most interspecific matings occur during the teneral period, before the integument is hardened and effective rejection of males is possible.

Coleoptera

Recognition devices are discussed later in an extensive review of mating behaviour in the Coleoptera (Section 5). These will be briefly summarised here. Visual stimuli, acoustic signals and long range pheromones are known to be used in the Lampyridae, Scarabaeidae (Rutelinae), Cerambycidae, Cantharidae and Scolytidae. Short range pheromones, contact chemoreception, close range acoustic signals and tactile signals are common in species found in substrate habitats (e.g. Staphylinidae, Silphidae and some Carabidae). The specificity of the signals varies in different species; those exchanged at close range are more specific, whilst long range signals generally serve to aggregate the sexes and are of limited specificity. It is rare to find cases in the literature where allopatric and sympatric species pairs have been compared; however, it is likely that the geographical distribution and ecology of the species in question, will influence the types of signal used for recognition.

Having discussed the types of recognition devices which are utilised by the major insect orders, only one type of device will now be considered in the Staphylinidae. These are the secondary sexual features of the males, particularly those which are likely to play a role in specific mate recognition and are thought to operate through the tactile mode.

The cuticle of insects is pre-adapted for structural modification, such as those incorporated in many for putative tactile recognition devices. That modifications may be employed in this way may be suspected when the structures are appropriately situated so that they would come into contact with receptors borne by the opposite sex during mating. Structures of this type should satisfy the following conditions. Firstly, tactile recognition devices should not be explicable in terms of other functions, and secondly, differences

are often accentuated between closely related sympatric species. For example, a structural modification of purely mechanical function, (assuming it is best adapted to its function), would not exhibit appreciable differences, outside the normal range of variation, between different species. Thirdly, tactile recognition devices should exhibit limited intra-specific variation but should be distinct from closely related sympatric species. Finally, structures of this kind are most often found only in males and cannot be explained in terms of co-adaptation with any female structures with a correspondingly limited variation.

In pairs of closely related pairs of partially sympatric species, it is likely that natural selection acts to limit the variation of a recognition feature within the area of overlap. However, beyond that area, in the absence of strong selection against heterogametic matings, there may be increased variation and "dialects" may occur (Littlejohn, 1965). Dialects are most often referred to in terms of song, (e.g. in the Orthoptera). This phenomenon is investigated in Quedius mesomelinus Marsh. and Q. maurus Sahlb., a pair of closely related species with a partially overlapping distribution (Section 6).

The Staphylinidae are a species-rich group of organisms in which male secondary sexual features which may be used as tactile recognition devices are of common occurrence, and it is for this reason that the present work has concentrated on the different types found in this family. Particular emphasis has been placed on comparing closely related sympatric and allopatric species. Species which exhibit features of this kind often have other general characteristics in common:- As the female stands to lose from an inappropriate mating she is coy. Manning (1966) regards this as a selective advantage. Males and females of many closely related

sympatric species are known to meet, but hybridisation between them is virtually unknown in nature. In ecological terms such species appear to break Gause's principal since they are able to coexist in the same habitat. Hence, as MacArthur (1972) and Hanski (in press) suggest, this is only possible if the resources of the habitat are randomly distributed. Habitats such as fungi, dung, compost and vegetable refuse heaps, where staphylinids are commonly found, could be considered as representing such patches, which are also of a heterogeneous nature.

Considering the size of the Order Coleoptera, very little observation has been made of mating behaviour. Where information is available, the concept of specific mate recognition has largely been ignored. In the present work, all the available information on mating behaviour from the literature and from personal observation is gathered together. Specific mate recognition is considered throughout the Order, and more particularly within the family Staphylinidae in relation to the role of secondary sexual features. Closely related allopatric and sympatric pairs are examined to gather evidence for the Wallace Effect. Where this is suspected to have been in operation, the phylogenetic relationships of the species concerned are examined, to establish the closeness of their relationship. Information of this nature may enable the pathway of speciation and the way in which development of the reproductive barriers occurs to be established.

SECTION 2

MATERIALS AND METHODS

2.1 COLLECTION OF SPECIMENS

Living adult Staphylinidae for behavioural work, and larvae for rearing, were obtained by collecting in the field throughout the year. The most efficient method for the collection of large numbers of specimens was to sieve compost, grass cuttings, dung and other debris using a coarse-meshed sieve. The sievings were placed in coarse-mesh bags in a Winkler funnel and the extracted specimens decanted at frequent intervals. Sorting at the time of sieving, while more selective, was less efficient and more time consuming.

2.2 REARING AND CULTURING

Adults were identified, sexed and placed singly into clear perspex boxes (55 x 35 x 20 mm and 80 x 45 x 20 mm, with a 5 mm diameter mesh covered hole at one end). The bottom of each box was covered with a layer approximately 5 mm deep, of damp potting compost, except for a small compost-free area at one end. A number of different substrates were provisionally employed including sand, decaying debris from the original habitat and filter paper. Commercial potting compost proved to be the most satisfactory since it retained moisture and enabled beetles to burrow through it. A small quantity of food material was placed in the compost-free area. Several different food materials, including Calliphora larvae, were utilised and cat food was found to be most suitable. Moistening of the substrate and replacement of food was necessary twice a week. A rather restricted fungal growth^{occurred}, which if left often resulted in the death of the beetle. Cultures were maintained at 16°C and 12 hr/24 hr light regime.

Single larvae, mainly of Quedius and Philonthus, were placed in similar boxes, substrate dampened and fed with one severed Calliphora larva or pupa every two days. When the larva pupated, the pupa was kept in the same box;

the potting compost moved to one end and the pupa placed on a square of damp filter paper in the cleared area. The filter paper and substrate was dampened occasionally, moisture levels being particularly critical at this stage. Larvae and pupae were maintained at a 20°C and 16 hr/24 hr light regime. These conditions promoted rapid development. Emerging adults were moved to a 16°C and 12 hr/24 hr light regime; the lower temperature was found to give a longer survival time in adult beetles.

This method was found to be suitable for most Staphylinidae, although species of Quedius, Philonthus, Tachinus and Tachyporus were most frequently cultured. Some difficulty was encountered in culturing Tachyporus, since it was found that moisture levels were more critical, the species requiring somewhat drier conditions. A more suitable food material was found to be a mixture of bran flakes and yeast extract.

2.3 SCANNING ELECTRON MICROSCOPY

Dried Museum specimens were used, either whole or with the relevant parts dissected under a stereoscopic microscope. This type of material generally required cleaning and several degreasing agents including mild detergent and acetone were utilised in conjunction with ultrasonic vibration or immersion in liquid nitrogen. The most successful method involved ultrasonic vibration in mild detergent for only 30 seconds, which prevented the destruction or removal of fine structures. This was followed by soaking in acetone and air drying. Cleaned specimens were fixed to stubs using araldite epoxy adhesive and placed overnight in an oven at 45°C, to harden.

Stubs were coated in a Polaron Equipment Ltd., S.E.M. coating unit, E 5000, with two 30 sec. coatings of 12 nm gold palladium. Specimens were examined with Cambridge Stereoscans 600 (15 Kv), Mark IIa (18 Kv) and 180 (15 Kv).

2.4 TRANSMISSION ELECTRON MICROSCOPY

This was employed for the examination of the internal structure of peg setae which are situated on the lateral lobe of the male genitalia. Dissected lateral lobes were embedded in araldite, trimmed into blocks and prepared for sectioning. Transverse sections were cut on a microtome with a glass knife, placed on carbon coated grids and stained with uranyl acetate and lead citrate. Sections were examined using an ASSOCIATED ELECTRICAL INDUSTRIES E.M. 6B.

2.5 PHOTOGRAPHY

Sequences in mating behaviour were photographed using a Nikon camera with 35 mm lens and bellows, Nikon Motor Drive and Speed Flash at 5 frames per second. Photographs were taken in daylight, with Ektachrome E6 64 ASA film from which Kodak reversal prints were obtained.

2.6 HISTOLOGY

Specimens were dissected and stored in distilled water and then subjected to the following procedure.

1. Transfer to 80% alcohol - 12 hours.
2. Soaking in diaphenol substitute solution: 50% acetic acid in which is dissolved potassium chlorate and hydrochloric acid. This yields chlorine dioxide in solution which breaks down and softens chitin. This took two to three days or until the specimen became colourless.
3. Transfer to 80% alcohol - 1 hour.
4. Transfer to 96% alcohol - 1 hour.
5. Transfer to isopropyl. alcohol - 12 hours.
6. Soaking in methyl benzoate celloidin - 12 hours.
7. Wash in xylene.
8. Soaking in toluene and paraffin wax - 1 hour.
9. Soaking in pure paraffin wax - 1 hour.
10. Renew solution of pure paraffin wax.

11. Embed and microtome 8 μ sections T.S. and L.S.

2.7 DRAWINGS

Outline drawings were made using a Wild M5 Stereomicroscope with Drawing Tube.

2.8 DISSECTION AND STORAGE OF MATERIAL

Dissections of genitalia were carried out using dried Museum specimens. The dissected parts were retained by mounting directly onto the card adjacent to the specimen, or placed in a micro-vial in glycerine which was attached to the specimen pin.

Specialised methods are discussed in the relevant sections.

SECTION 3

THE STRUCTURE OF THE GENITALIA

3.1 STAPHYLINIDAE

The female genitalia in most cases consists of comparatively slight modifications of the eighth, ninth and tenth abdominal segments and their appendages (Blackwelder, 1936). However in the Tachyporinae in particular there is considerable modification of the eighth tergite and sternite. The ninth abdominal segment in the female generally forms the genital segment, the sternite of which is divided into a pair of hemisternites between which the vulva is situated. The ovipositor is formed by the stretched eighth and ninth abdominal segments which are telescoped at rest (Tuxen, 1956). Similarly, the ninth abdominal segment is generally the genital segment in the male, the genital tube being composed of sclerites and membranes arranged around the terminal portion of the ejaculatory duct (Tuxen, 1956). The sclerites of the genital tube consist of two main parts, divided by a connecting membrane: the first is the median lobe which is the apical portion of the tube containing the terminal portion, or internal sac, and the ejaculatory duct orifice, the second is the tegmen consisting of the basal sclerite and the lateral lobes. The male genitalia of Staphylinidae are characterised by a highly developed median lobe, absence of a basal sclerite and great variety in form of the lateral lobes (Sharp & Muir, 1912). Members of the Staphylinine tribes Platyprosopini, Diochini and Othini have the more primitive form of genitalia for the sub-family with two separate lateral lobes; the Xantholinini, while also having separate lateral lobes when they are present, possess a considerably specialised median lobe. These are discussed in greater detail in Section 7.

3.2 STAPHYLININI

The present thesis concentrates on the Staphylinini. As in most Staphylinidae the genitalia are of the "articulate" type (Tuxen, 1956),

with the lateral lobes usually united into a single lobe, or paramere, which articulates directly by true condyles to the ventral surface of the median lobe. The median lobe has a large bulbous base and bears the median orifice at its distal end. On the ventral surface, at the junction of the bulbous part and the distal tube, is the small median foramen through which the ejaculatory duct passes (Blackwelder, 1936). The median lobe contains the internal sac (terminal portion of the genital tube) which is everted during copulation through the median orifice. The membranous walls of the internal sac frequently bear an armature of spines, denticles, hairs, scales and papillae, which at rest project into the lumen of the sac. When the sac is everted they serve to fix onto the walls of female bursa copulatrix. This type of armature is often species specific (Tuxen, 1956). The ejaculatory duct opens to the exterior through the chitinised termination of the internal sac, the flagellum, which at rest is enclosed by the rest of the internal sac (Blackwelder, 1936).

The male genital tube exhibits modifications associated with the eversion of the internal sac. The basal bulb of the median lobe bears chitinised sclerites on the dorsal and ventral aspects, with a broad band of membrane between (the dorsal sclerite is referred to as the pressure plate). These sclerites are brought together by muscular contractions which exert pressure on the haemocoelic fluid resulting in the eversion of the sac (Sharp & Muir, 1912).

3.3 MUSCULATURE ASSOCIATED WITH THE GENITALIA

The musculature associated with the genitalia is figured in a representative species of the Staphylinini, Creophilus maxillosus L. after comparison with Staphylinus olens Muller, Philonthus cognatus Steph. and P. fimetarius (Grav.) (Figs 3.1-4). The arrangement of the muscles was found to be essentially similar with only slight differences, in the species examined. Seevers (1978) figures the genital musculature of the Aleocharinae.

The muscles shown in the annotated diagrams (Figs 3. 1-3.4) are those concerned with;

- (a) the movement of the aedeagus into and out of the abdomen
- (b) the rotation of the aedeagus from the resting position to the copulatory position. At rest the median lobe lies laterally in the abdomen in many members of the Staphylininae, and is rotated into a ventral position, with the lateral lobe dorsal, prior to copulation (see Section 7).
- (c) the eversion of the internal sac resulting from the contraction of the basal bulb of the median lobe by compression of the pressure plate.

Muscles concerned with the invagination of the internal sac, after intromission, are located within the basal bulb and are attached directly to the internal sac. These are not included. Seevers (1978) figures the internal genital musculature of the Aleocharinae. It is likely that, in addition to the specialised musculature, the general abdominal musculature is also involved in extrusion of the genitalia since, in relaxed or freshly killed specimens, slight pressure on the apical tergites results in extrusion of the genitalia.

The lateral lobes are generally united into a single lobe and exhibit extreme, sometimes bizarre, modifications. These are illustrated (Section 4) and further discussed (Section 7). The position of the lateral lobe/s in repose in the abdomen, the shape of the median lobe and abdominal apex are discussed in relation to mating position (Section 7).

On the internal surface of the lateral lobe, i.e. that facing the median lobe in the Staphylinini, are short, stumpy macrotrichia which will be referred to as peg setae. The distribution of such peg setae is often characteristic of individual species.

Fig.3.1. Dorsal dissection of musculature associated with the genitalia in Creophilus maxillosus.

Stage 1

Specimens had been stored in 80% alcohol and dissection was completed in the same solution. The musculature could be seen particularly well in this type of material.

Tergites VII, VIII and IX were removed along with the general abdominal musculature, fatty tissue, hind gut and accessory glands.

The muscles of the genitalia lie over the second connecting membrane which is attached to the basal bulb of the median lobe and forms the lining of the chamber in which the aedeagus lies. The part of the aedeagus within the membrane chamber is effectively exterior.

muscles which evert the internal
sac by compression of the pressure
plate exerting hydrostatic pressure

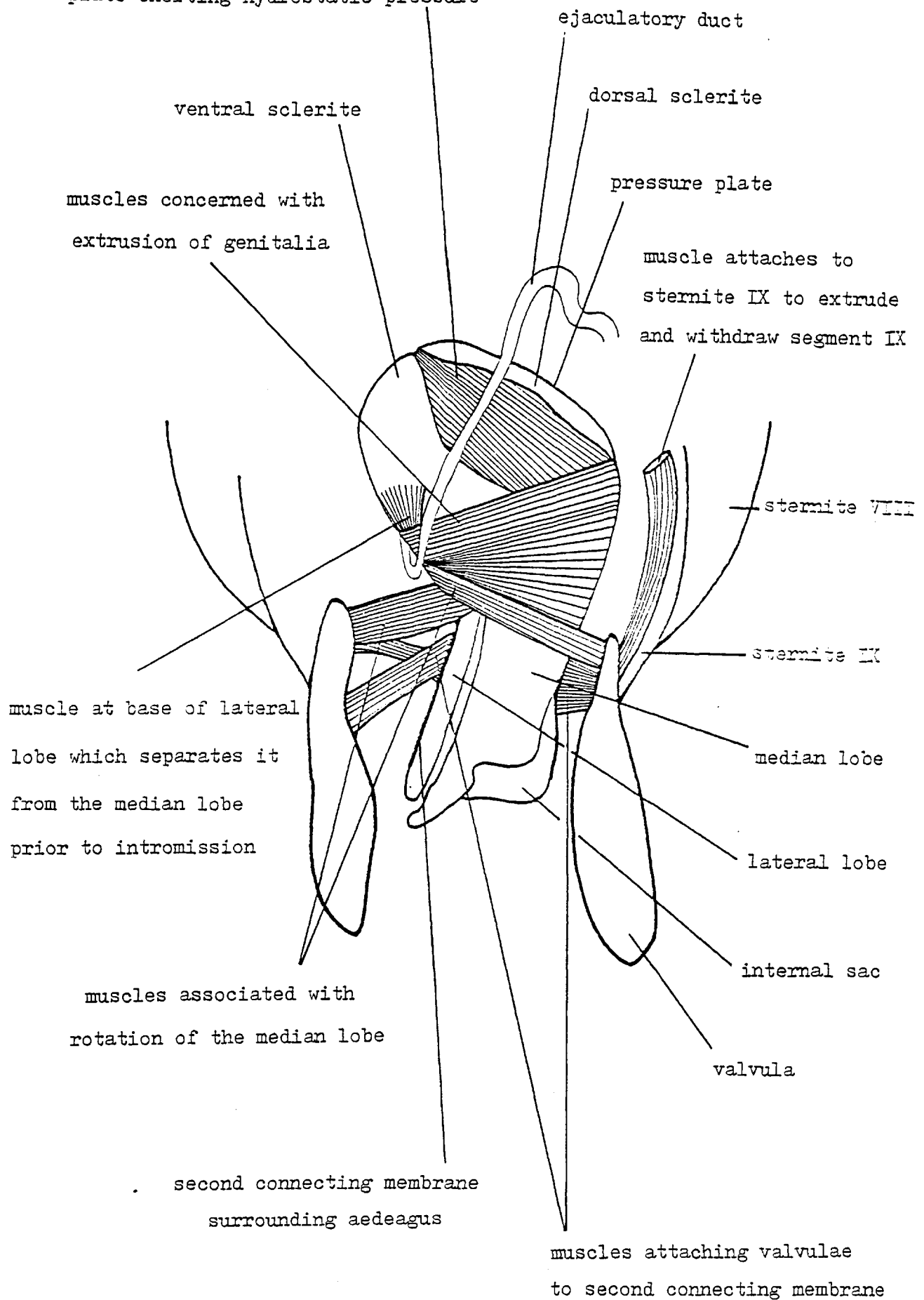


Fig.3.2. Dorsal dissection of musculature associated with the genitalia in Creophilus maxillosus.

Stage 2

The top layer of muscles overlying the second connecting membrane ~~was~~ removed along with much of the membrane itself.

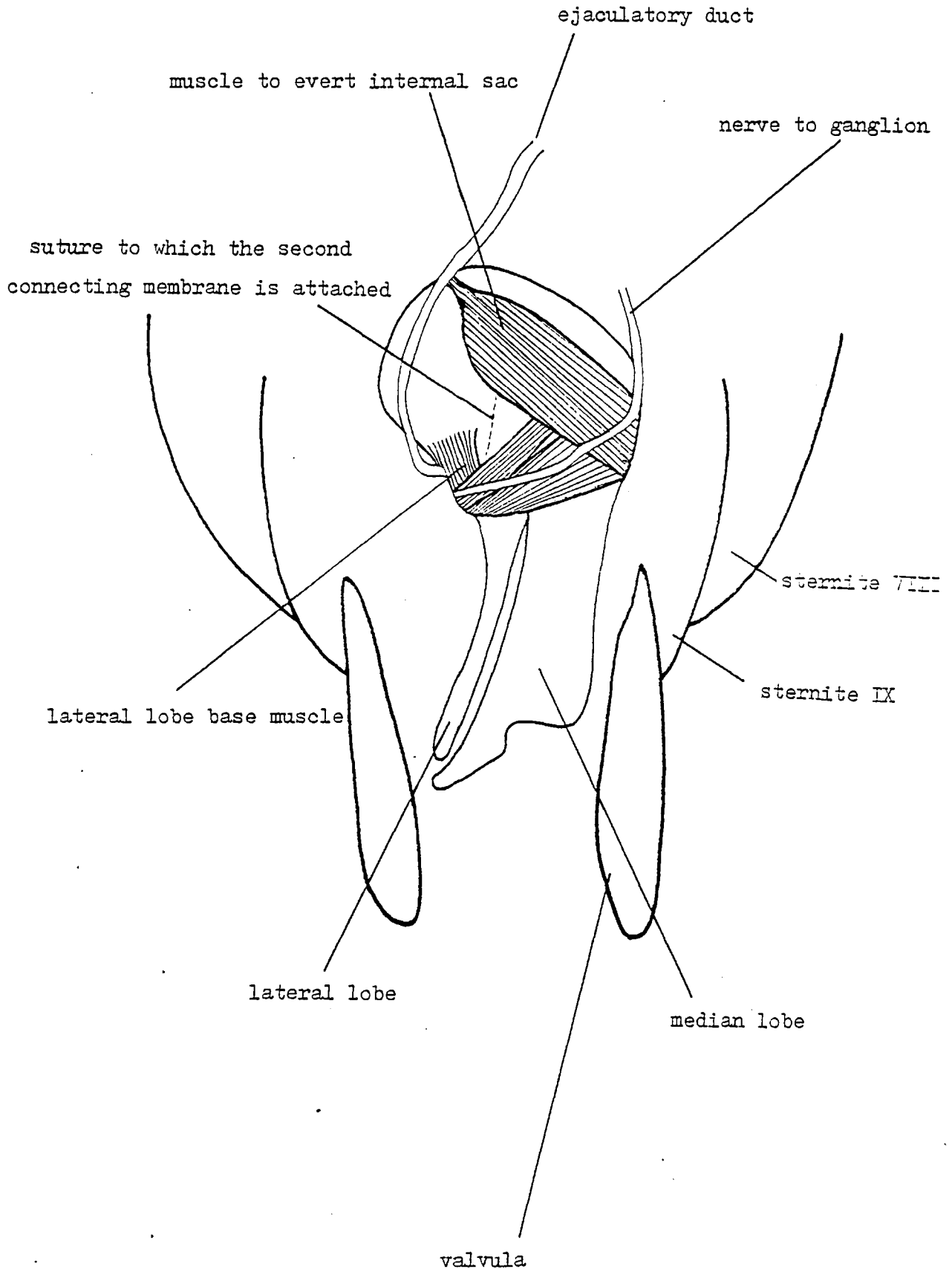


Fig.3.3. Dorsal dissection of musculature associated with the genitalia in Creophilus maxillosus.

Stage 3

A further layer of muscles ~~was~~ removed from around the aedeagus.

membranous division between dorsal and ventral sclerites
to which second connecting membrane is attached

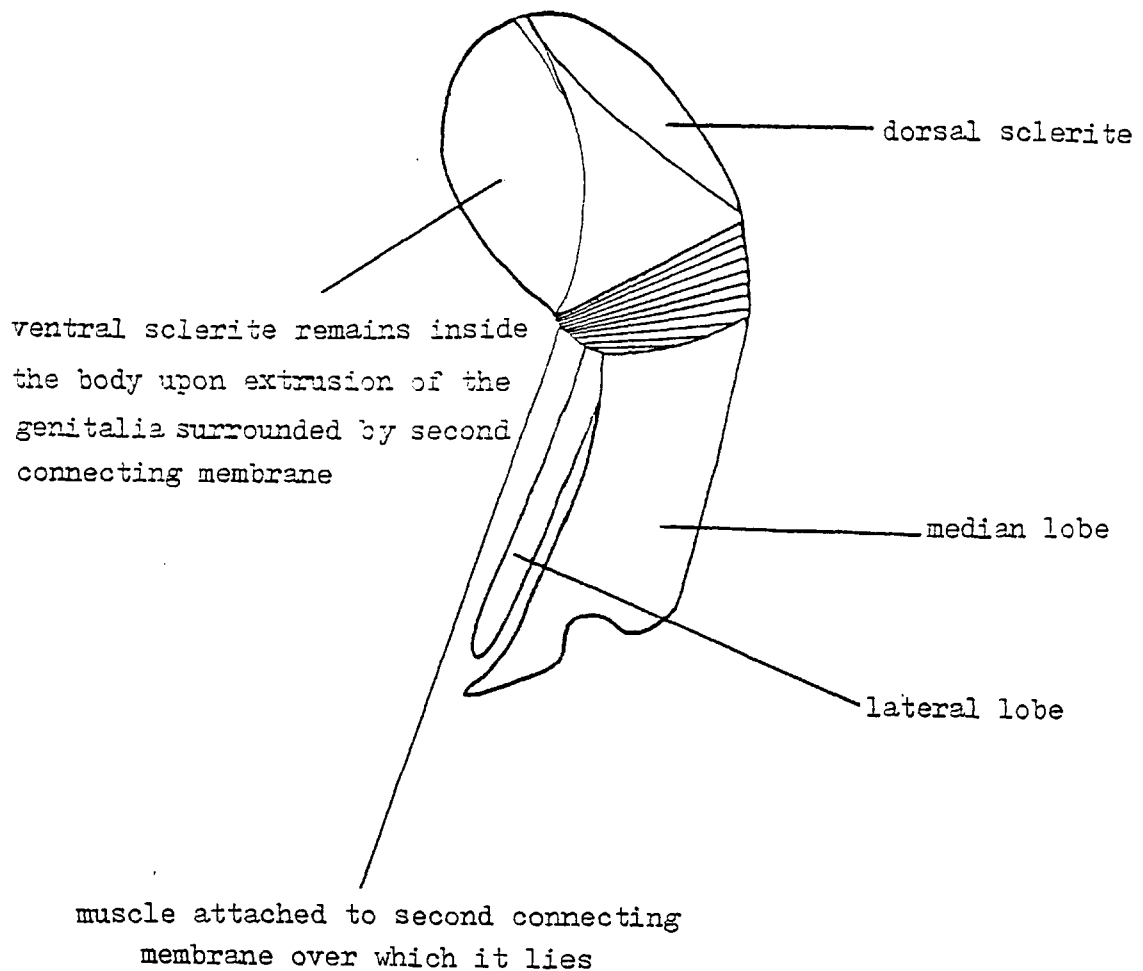
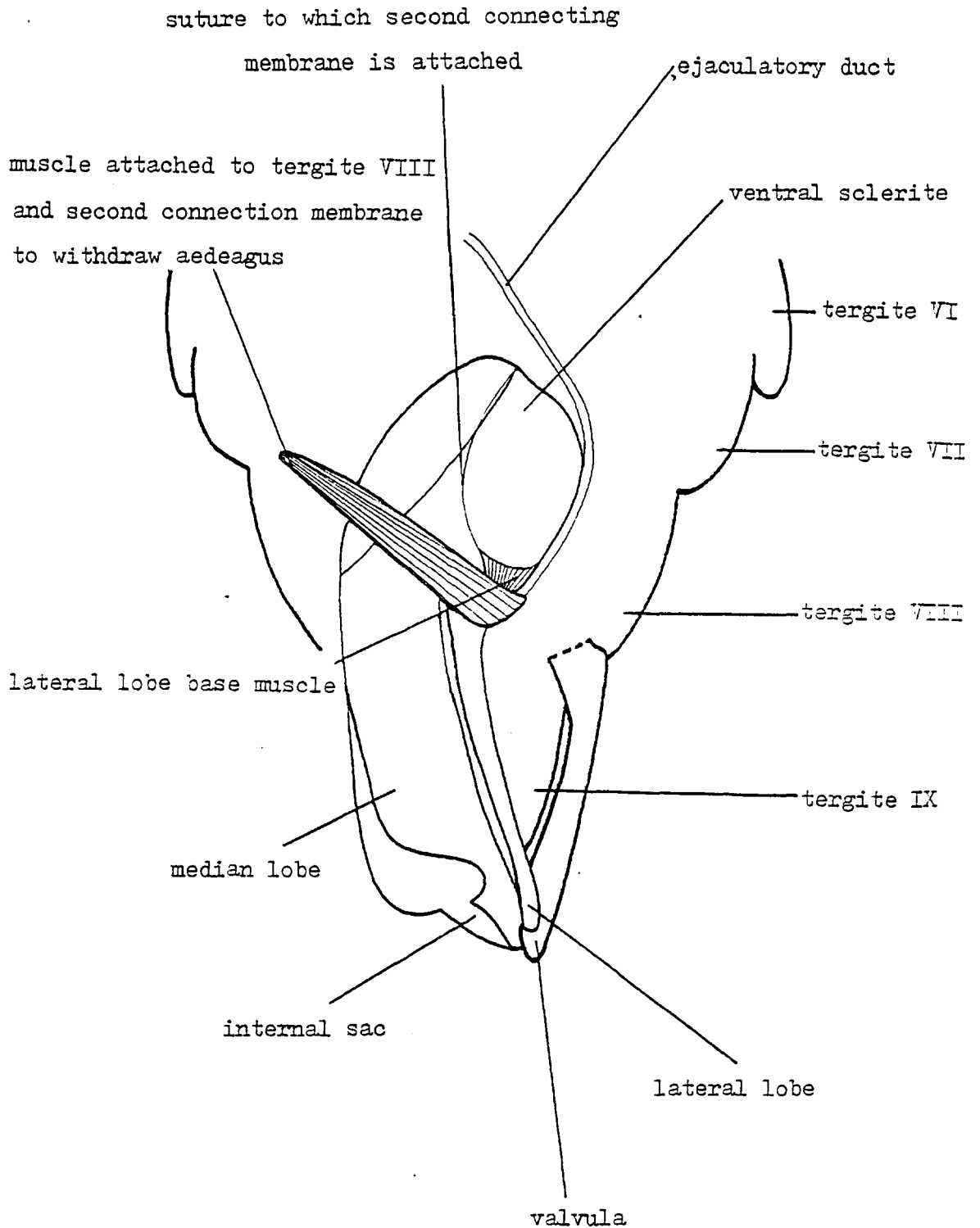


Fig.3.4. Ventral dissection of musculature associated with the genitalia in Creophilus maxillosus.

Sternites VI, VII, VIII and IX were removed along with general abdominal musculature, associated membranes and fatty tissue.



3.4 STRUCTURE AND FUNCTION OF PEG SETAE

The micro-structure, distribution and possible function of peg setae has been discussed by Hammond (1972a) and is further investigated in the present thesis.

Transverse and longitudinal serial sections of the lateral lobe of Philonthus sordidus (Grav.), examined by Transmission Electron Microscopy (TEM) and Light Microscope (LM), revealed a structure for peg setae which is likely to be similar to that of filiiform setae. They are socketed at the base with distinct surface sculpturing similar to that found in many filiiform setae which occur in both sexes of Coleoptera and other insects (Hammond, 1972a). (Plates 3.1-3.3). The size and shape of the peg setae vary with their siting and, as discussed later (Section 4), setae of this type may occur on legs, and various abdominal segments as well as on the genitalia. Different shapes of peg setae may occur in close proximity, e.g. Philonthus pellax Tott. and P. cinctipennis Fauv., where rounded and tooth-like pegs are found together on the lateral lobe. In more elongate peg setae (e.g. those found on the abdomen of Tachinus spp., Plate 3.8) the sculpturing consists of ridges which run parallel with the sides (Plate 3.4-3.7). Here, the peg is bilaterally symmetrical and ridges running along the two sides of the peg terminate and interlock apically in the mid line. In the shorter rounded peg setae, most typical of the lateral lobes of the male genitalia in the Staphylinini, sculpturing follows a similar pattern, although the ridges may meet to one side of the apical mid line, (Plate 3.4-3.7). Close examination, using the SEM, of the surface of peg setae found on the lateral lobes of some Philonthus spp. did not reveal any further micro-sculpturing or the presence of pores, (Plate 3.5). TEM and LM studies revealed that these peg setae have a solid internal structure, (Plate 3.1). It is also apparent that the lateral lobe has a thick cuticle but is hollow along its length. Associated with sensory filiiform setae on the lateral lobe

there are channels in the surface cuticle which lead to the setal socket. It is probable that a channel of this type contains the setal nerve cell which connects with a series of nerve fibres in the hollow centre of the lateral lobe. Wigglesworth (1972) discusses the nerve supply to similar sensory filiform setae. Similar channels also run to the sockets of the peg setae indicating the possibility that these are innervated, (Plates 3.2 and 3.3). Owing to their solid structure and the absence of sieve like pores, a chemosensory function for peg setae appears to be ruled out. Hammond (1972a) suggests one function of such peg setae is in courtship and mating, since they only occur in males and their siting is frequently species specific, being situated at points on the body surface where they are likely to come into contact with female receptors. Continued investigations in the present thesis are designed to test the validity of this view. Additional information, gained from studies on mating behaviour (Section 5), and ultrastructure point to their function as species specific tactile recognition signals. These are received by the female as a last stage in a sequence of behavioural events during courtship to elicit a receptive response to a conspecific male. They may also be used as mechanoreceptors by the male as a stimulus for specific events during mating. The peg setae lie on the female ninth tergite during intromission and this lacks any specific structure, other than sensory setae, onto which the peg setae could hook. It is unlikely that there would be marked divergences in pattern between closely related sympatric species if the sole function of the peg setae was mechanical. It is not known whether the sculptured surface affords any grip on the female. There seems to be good evidence to support the hypothesis that peg setae are modified mechanoreceptors, as are other setae on the genitalia which stimulate successive stages of copulation, such as the lateral lobe apical setae of the Staphylinini which are likely to be used in preliminary orientation of the genitalia. Although it is likely that their function

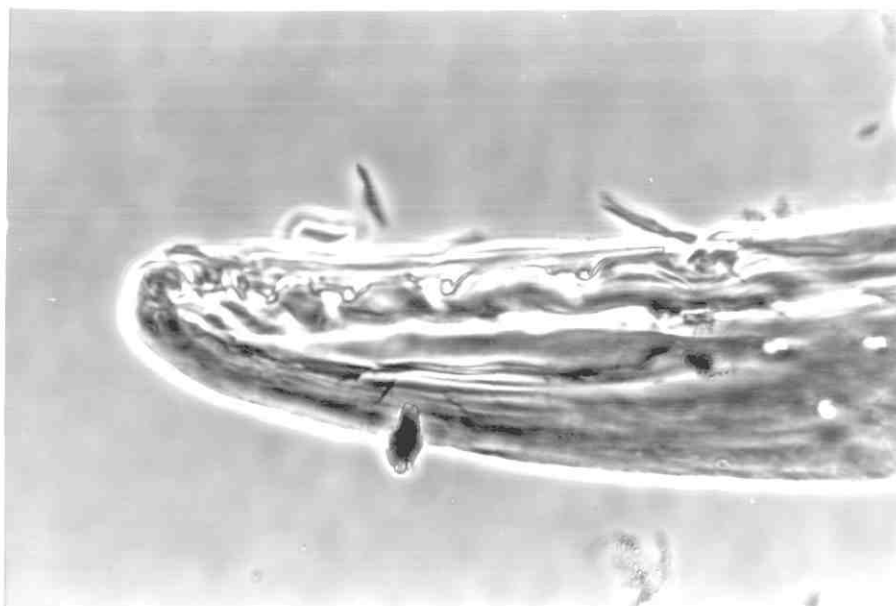
as mechanoreceptors is now redundant, morphological evidence indicates that peg setae are structures of a type which are ideally situated for development into a specific tactile signalling system to be used at close quarters. Further evidence may arise from groups of closely related allopatric species where peg setae are absent, or from cases of closely related species groups where lateral lobes of individual species lack peg setae, in groups in which such structures are common.

Plate.3.1. Transmission electron micrograph of a transverse section through the lateral lobe and peg seta of the male genitalia of Philonthus sordidus.



Plates.3.2.- 3.3. Light micrographs of longitudinal sections through the lateral lobe of the male genitalia of Philonthus sordidus, to show the sockets of the peg setae.

3.2



3.3



Plates.3.4 - 3.8. Scanning electron micrographs of male peg setae.

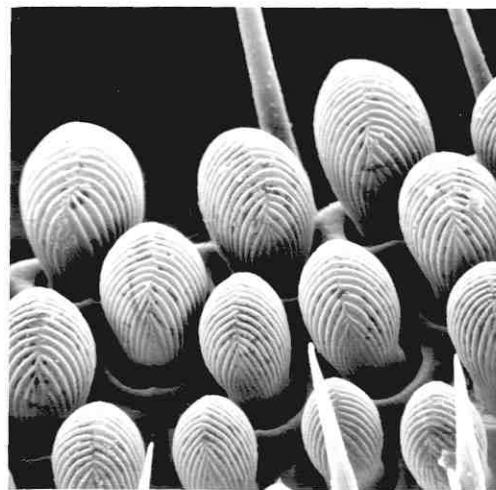
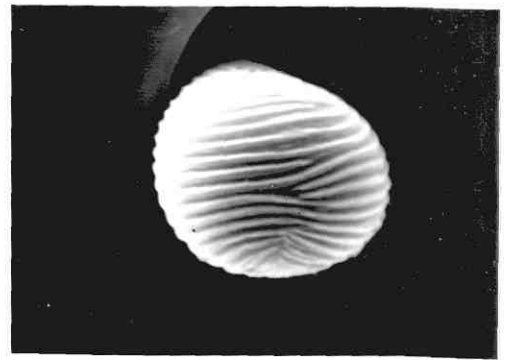
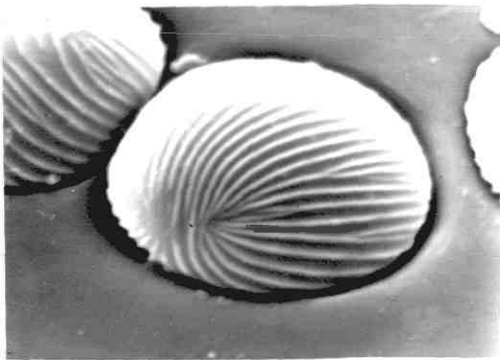
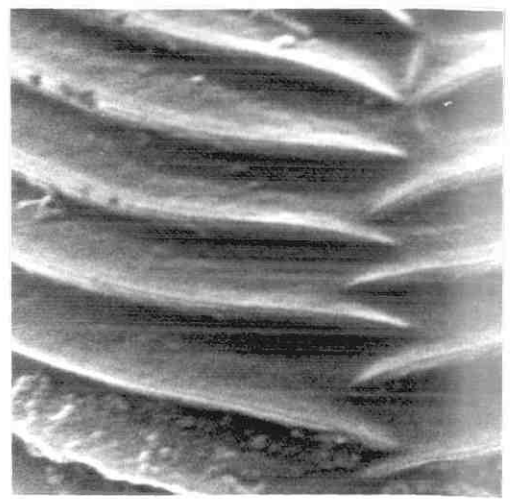
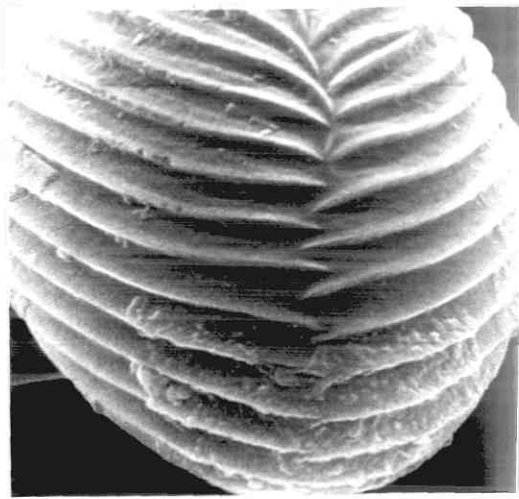
3.4. Peg seta of male sternite VII of Tachinus humeralis
(x 3000)

3.5. Peg seta of male sternite VII of Tachinus humeralis
(x 6000)

3.6. Peg setae of male lateral lobe of Philonthus
cephalotes (x 3000)

3.7. Peg seta of male lateral lobe of Quedius maurus
(x 3000)

3.8. Peg setae of male sternite VII of Tachinus
humeralis (x 600)



SECTION 4

SURVEY OF SECONDARY SEXUAL FEATURES IN THE STAPHYLINIDAE

INTRODUCTION

Secondary sexual features are commonly regarded as being those peculiar to one sex, which are not concerned with the primary functioning of the sexual organs themselves. The present discussion extends to include structures associated with the male genitalia which play other than purely mechanical roles in mating, and includes comment on features of the internal sac of the male genitalia where these exhibit marked differences between closely related species.

The discussion is concerned with two issues; the identification of features which may be involved in the production of tactile signals, and the demonstration that these features are unusually divergent in some pairs of closely related species. Although related, the distinction between these two issues is an important one. Only the second is able to provide evidence for the Wallace Effect.

4.1 CLASSIFICATION OF SECONDARY SEXUAL STRUCTURES

Secondary sexual structures may be classified primarily according to their functions and secondarily according to their siting and composition.

1. Structures involved in division of labour.

Co-operative efforts between males and females may produce sexual dimorphisms which are marked. These are particularly noticeable in those tunnelling and burrowing species where there is co-operation between the sexes to prepare brood galleries for their offspring. Modifications may occur in the mandibles and legs which are used for digging. However, any difference in general male and female role may involve dimorphisms which are not directly concerned with reproduction. In the "ambrosia" beetles (Platypodidae) structural differences occur which are associated with the carrying and spreading of the fungus with

which they line their tunnels for food. Modifications of the female associated with oviposition should be briefly mentioned. These include increased rostrum length in some Curculionidae, narrowing and strengthening of the terminal segments of the abdomen, and adaptation of the legs for digging and ovipositing into particular substrates.

2. Structures which play a "mechanical" role in mating.

Males have various adaptations which enable them to grip the female during mounting. These include modification of mandibles as in Dorcus and Lucanus (Lucanidae) (Section 5.5.2.10), the shape of the legs, particularly the pro-tarsi (and sometimes other tarsi) which become expanded with their ventral surfaces bearing sucking discs, e.g. Dytiscidae, Gyrinidae, and Hydrophilidae, or other adhesive setae, e.g. Carabidae, Staphylinidae and other families (Stork, 1980). Females are sometimes co-adapted with ridged or granulate elytra to enable the males to hold them securely. In the Tenebrionidae, Eleodes hispilabris Say and E. connexa Lec. males bear a short pointed pre-apical spur on the pro-thoracic femur which hooks onto a protuberance on the female elytra. Similarly in Tenebrio molitor L. the male legs hook onto the female elytra (Doyen, 1966; August, 1971; and Gerber, 1973). The males of individual melyrid species have modified second pro-tarsal segments which are pectinate and used to anchor onto the female (Matthes, 1971). In Androchirus spp. (Tenebrionidae) the male eighth sternite is modified to hold the female abdomen and guide the genitalia to the gonopore (Campbell, 1966). The antennae of male Collops vittatus Say (Melyridae) have a depression in the anterior surface of the enlarged segments in which the female mandibles are held during courtship (McAtee, 1916, Nielson & Henderson, 1959).

Other families exhibit a variety of developments of the antennae which serve a gripping function and many parts of the male ventral surface may be modified for the same purpose.

3. Structures which play a role in sensory reception during mating.

Structures of this type may or may not be specific and are sometimes concerned with the appropriate functioning of the genital organs e.g. tactile setae on and around the male genitalia. Included, also, are those structures which are concerned with the location of a mate by olfaction, particularly in cases where the female produces a pheromone during the mating period. This coincides with development of the male antennae where the flagellum is elongate or plumose. Examples are seen in the Buprestidae; Xenorhipis, Hesperorhipis, and Trichinorhipis and in the Rhipiphoridae.

4. Structures which play a role in specific mate recognition.

This category can be further subdivided to include the different aspects of specific mate recognition.

a) Intra-sexual Selection.

1. production of non-tactile signals.

These characters, usually found in males, are purely ornamental and may be used during courtship display between rival males in the presence of a potential female mate. Such characters include the male horns and thoracic development in the Lucanidae, Scarabaeidae, and Tenebrionidae, and the enlargement of the head and pronotum in male Staphylinidae.

b) Intra-specific epigamic selection.

Wilson (1975) discusses different aspects of intra-specific epigamic selection.

1. production of non-tactile signals.

The enlargement of the fore-parts in the male Staphylinidae, mentioned in the preceding category may also be concerned with epigamic selection. Structures involved in intra-sexual selection and epigamic selection may be difficult to distinguish. Structures which form

part of an attractant device are included here. The antennae of male Pleuropompha (Meloidae) bear pores from which a chemical attractant is secreted; fanning of the antennae during courtship assists the evaporation and dispersal of the chemical to the female (Pinto, 1973).

In the Melyridae, malachiine males possess cranial and elytral secretory excitator organs which are presented to the female during courtship. Similarly males of Lytta spp. (Meloidae) bear cranial pits containing short setae from which a secretion is produced. The secretion stimulates the female when her antennae are pressed into the pits.

2. production of tactile signals.

i) from a non-specific structure.

These include structures which are used to "stimulate" or "pacify" the opposite sex during mating. Pterostichus (Carabidae) males bear a protuberance on the seventh sternite which is rubbed on the female elytra as a specific stimulation to end her resistance to mating (Witzke, 1973). The enlarged mandibles of male Dorcus and Lucanus (Lucanidae), as well as being used for gripping the female, are also used to "subdue" her (Mathieu, 1969). Mechanical stimulation is achieved using saw-like antennae in males of Anthocomus fasciatus L. (Melyridae) (Matthes, 1971).

ii) from a specific structure.

Characters of this nature are of the greatest interest in the present thesis, and have been examined in detail in the Staphylinidae. They may be regarded as tactile recognition devices, and satisfy the following conditions;

1. They are not explicable in terms of other functions.
2. Variation within a species is narrow.
3. They are not explicable on grounds of co-adaptation with any female structures, as, for example, a mechanical aid

during mating.

4. Differences are often accentuated between closely related sympatric species.
5. "Dialects" may occur beyond the areas of overlap.
6. Female receptors are suitably sited.

The aim of this survey in the Staphylinidae is to present examples from a number of different subfamilies to indicate the range of different types of features. The survey concentrates on groups where it is possible to make a comparison of closely related sympatric and allopatric species. An attempt is made to determine the precise function of such structures, particularly where specific mate recognition and/or reproductive isolating barriers are thought to be involved. Secondary sexual features of this type are to be found in species which predominate in certain ecological situations. Such situations exist where a habitat is highly heterogeneous enabling two or more closely related species to live in close proximity. Habitats of this kind are often transient with patchily distributed resources and include putrifying matter; rotting fruit, carrion, dung, nests, fungi, and synanthropic situations such as vegetable refuse and compost heaps.

Sympatric closely related or sister species are often virtually indistinguishable. However, where structures are present which are likely to be used at close quarters for specific mate recognition, these are frequently divergent. This provides evidence for the selection for assortative mating (Hammond, in press^b). Development of elaborate male secondary sexual characters is common under these circumstances. They are located on a part of the body with which the female would make contact during courtship and mating. Modification of the male posterior abdominal sclerites and of the apical genitalic processes are the most frequent features of this type. The female only exceptionally carries modifications of this kind and generally

remains virtually indistinguishable from females of other cohabiting species. In habitats where closely related species are broadly sympatric, but rarely syntopic, the differences between them are not so striking and are usually composed of slight modifications of a basic structure, i.e. comparative differences. These differences are often confined to the apical processes of the genitalia. This is borne out when looking at some of the major staphylinid subfamilies.

In the Omaliinae numbers of closely related species are rarely found together even in putrifying habitats; they are mostly allopatric. There are some sympatric closely related species, e.g. in waterside species, but differences in genitalia are small and they lack marked secondary sexual characters of the tactile recognition type. The genus Acrolocha is an example of an exception to this (Section 4.3.2). Species of the Oxytelinae have marked secondary sexual characters which may be used as tactile recognition features, e.g. in Platystethus and Anotylus. In leaf litter dwelling species of Anotylus, appreciable inter-specific differences are rarely exhibited. However, exaggerated differences between closely related Anotylus species can be found in fruit, dung and carrion habitats where they occur together in numbers. This is illustrated by trapping results from the Royal Geographical Society (RGS) Expedition to Sarawak. 27 different species of Anotylus were collected from baited pitfall traps in a 10 mile diameter area of rain forest. Up to 9 different species, some closely related, were collected in one pitfall trap during one night (Hammond, pers. comm.). In general secondary sexual features of the putative tactile recognition type are poor in the Oxytelinae and differences between species are comparative. Closely related species which appear to cohabit are often separated by ecological differences, e.g. Bledius (the marked secondary sexual differences of the foreparts are unlikely to be tactile recognition features).

In the Steninae there are very few closely related syntopic species and secondary sexual features of the putative tactile recognition type are poor. Exceptions occur in Stenus provilus Fr., S. clavicornis (Scop.) and related species (Puthz, 1971). The Paederinae are a tropically centred group and although only relatively small numbers of species occur in putrifying habitats, closely related species cohabit, and hygrophilous and waterside species often have striking abdominal and genitalic characters of the tactile recognition type, e.g. in Lithocharis, Medon, Scopaeus and Lathrobium.

Species of the Staphylininae show striking secondary sexual features of the tactile recognition type. In temperate regions good differences are to be found in closely related species which inhabit synanthropic habitats, putrifying matter and dung. Species living in more homogeneous habitats, e.g. deciduous forest litter, tend to exhibit only comparative differences. An example of numbers of species occurring together in tropical situations is provided by data from the RGS Sarawak Expedition. 18 species of Philonthus were collected in baited pitfall traps over a 10 mile diameter area of rain forest. 5 species were collected together from the same trap and of these 4 species were virtually indistinguishable except for the male secondary sexual features (Hammond, pers. comm.).

4.2 CLASSIFICATION, BY SITING, OF THE SECONDARY SEXUAL CHARACTERS IN THE STAPHYLINIDAE

4.2.1 Head

In the male Staphylinidae (Staphylininae, Paederinae and Oxytelinae) commonly the head and fore-parts may be enlarged. This alters their shape to some extent. This may function in sexual selection since the expression of such characteristics may be extremely variable within one species. A number of species groups of Anotylus (Oxytelinae) exhibit such sexual dimorphism including a variety of horns, protruberances or other outgrowths. These modifications are found in species native to

the Neotropics, or the Oriental-Australasia region (Hammond, 1976).

Males of many species of Platystethus and Bledius (Oxytelinae) possess spines on the head.

4.2.2. Thorax

There is general expansion of the fore-parts including the development of pronotal horns in e.g. Bledius. Expansion again causes a change in shape which may affect the associated microsculpture. However, the principle secondary sexual structures of the thorax concern leg modification. In many male Staphylinidae the fore-tarsal segments may be expanded, their ventral surfaces bearing dense setae which aid in gripping the female during mounting. This may also involve the mid legs but rarely all three pairs of legs. Some more specific features are present in various subfamilies; either consisting of a modification in shape, or the possession of one or several modified, or peg-like, setae (Hammond, 1972a; and Section 3.4). These are reviewed in a number of subfamilies.

Micropeplinae.

Many species bear small, brown or yellowish peg setae on the male tibiae and these are similar in structure to those found in the Proteininae and Omaliinae. The mid and hind-tibiae of Micropeplus spp. and Kalissus bear setae of this type in association with the toothed and sinuate development of the segment (Campbell, 1968; Hammond, 1972a).

Proteininae.

The presence of small black peg setae, along with modification in shape of the male tibiae, are good species specific characters. All the Megarthus and Metopsia species in the BMNH collection possess leg peg setae. The five British Megarthus species, which are broadly sympatric, have been examined in detail (M. affinis Muller, M. denticollis (Beck), M. depressus (Payk.), M. hemipterus (Ill.), and M. sinuatocollis (Bois. & Lac.). The mid leg bears rows of peg setae, of variable

number, on the interior surface of the trochanter and tibia (Fig 4.1). The interior surface of the hind leg trochanter, except in M. denticollis and M. sinuatocollis, bears one to three peg setae, or in the case of M. depressus up to seven short sharp setae (Fig 4.2). The tibia of the hind leg, except in M. affinis, is much modified in shape and peg setae are borne on the interior surface (Fig 4.2.). Males of many Proteinus species possess similar peg setae or spines on the interior surface of the mid and hind trochanters, femora and tibiae (Figs 4.11 & 4.12). The five closely related British species of Proteinus, pairs or more of which are sympatric, are examined in detail in Section 4.3.1. Omaliinae.

Peg setae of a similar kind occur on the fore and mid tibia of males in some omaliine genera, including Amphicroum, Deliphrum, Arpedium, Pelecomalium, Camioleum and Eusphalerum. Males of two sympatric species of Acrolocha (A. sulcula (Steph.)) and A. minuta (O1.) have distinctly different hind trochanters. In A. minuta it is obliquely truncate externally, with the postero-external angle produced into a small outwardly directed tooth. In A. sulcula the hind trochanters of both males and females are simple (Fig 4.15e,f & g; Section 4.3.2).

Steninae.

The male hind tibia and femur of some species may be modified (Tottenham, 1954).

Staphylininae.

In the Gabrius hesperius - Group, a North African group of five species (previously described as only two species), the males possess very striking secondary sexual characters which distinguish otherwise morphologically very similar species. These characters include modification of the hind femur and tibia (Section 4.3.5).

Other thoracic secondary sexual characters are rare, although in the Tachinus silphaeformis group there is sexual dimorphism in the

Fig.4.1 Male meso-thoracic legs of Megarathrus, bearing peg setae on the trochanter and tibia, a) M.depressus, b) M.sinuatocollis, c) M.affinis, d) M.denticollis, e) M.hemipterus.

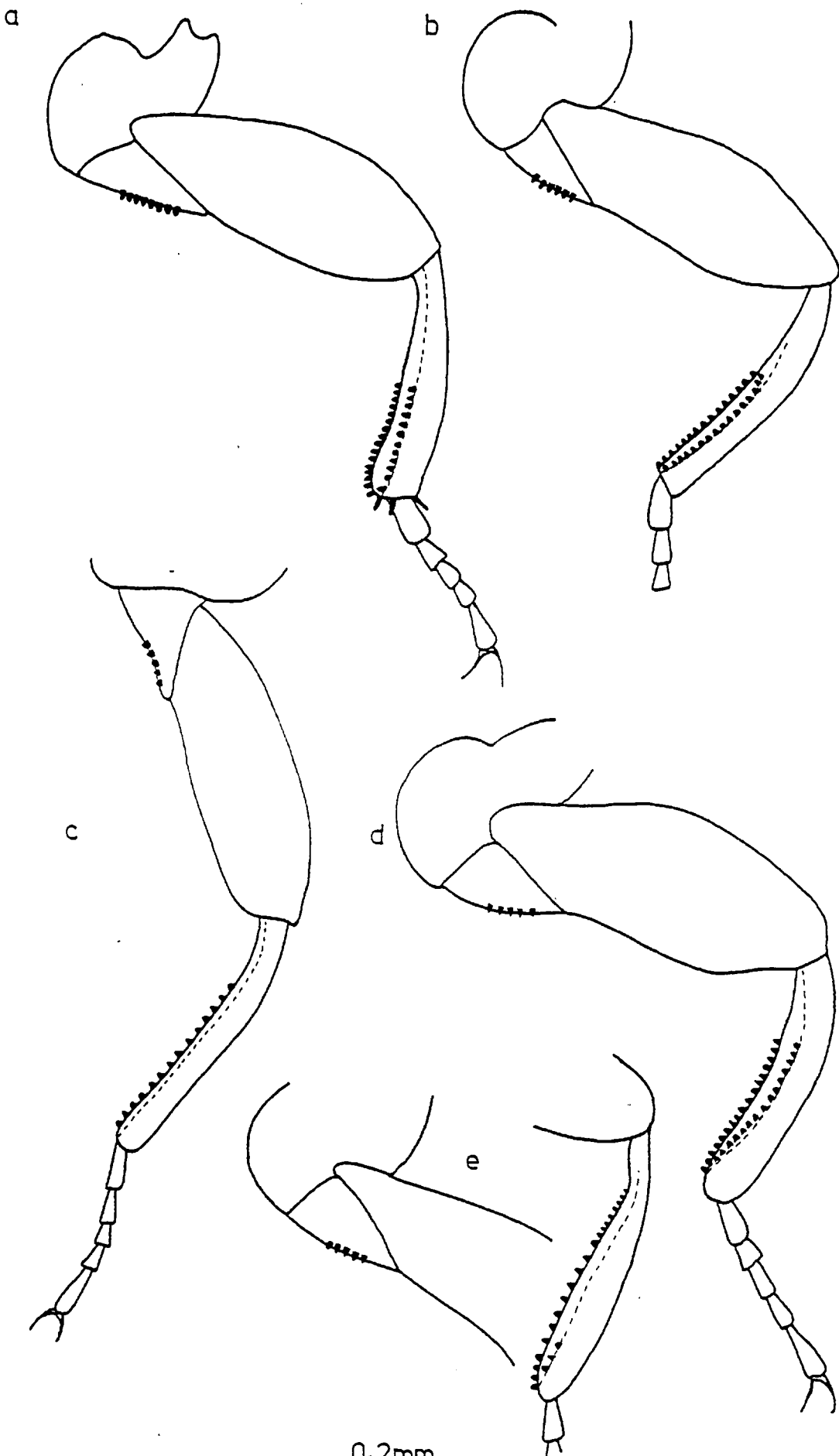
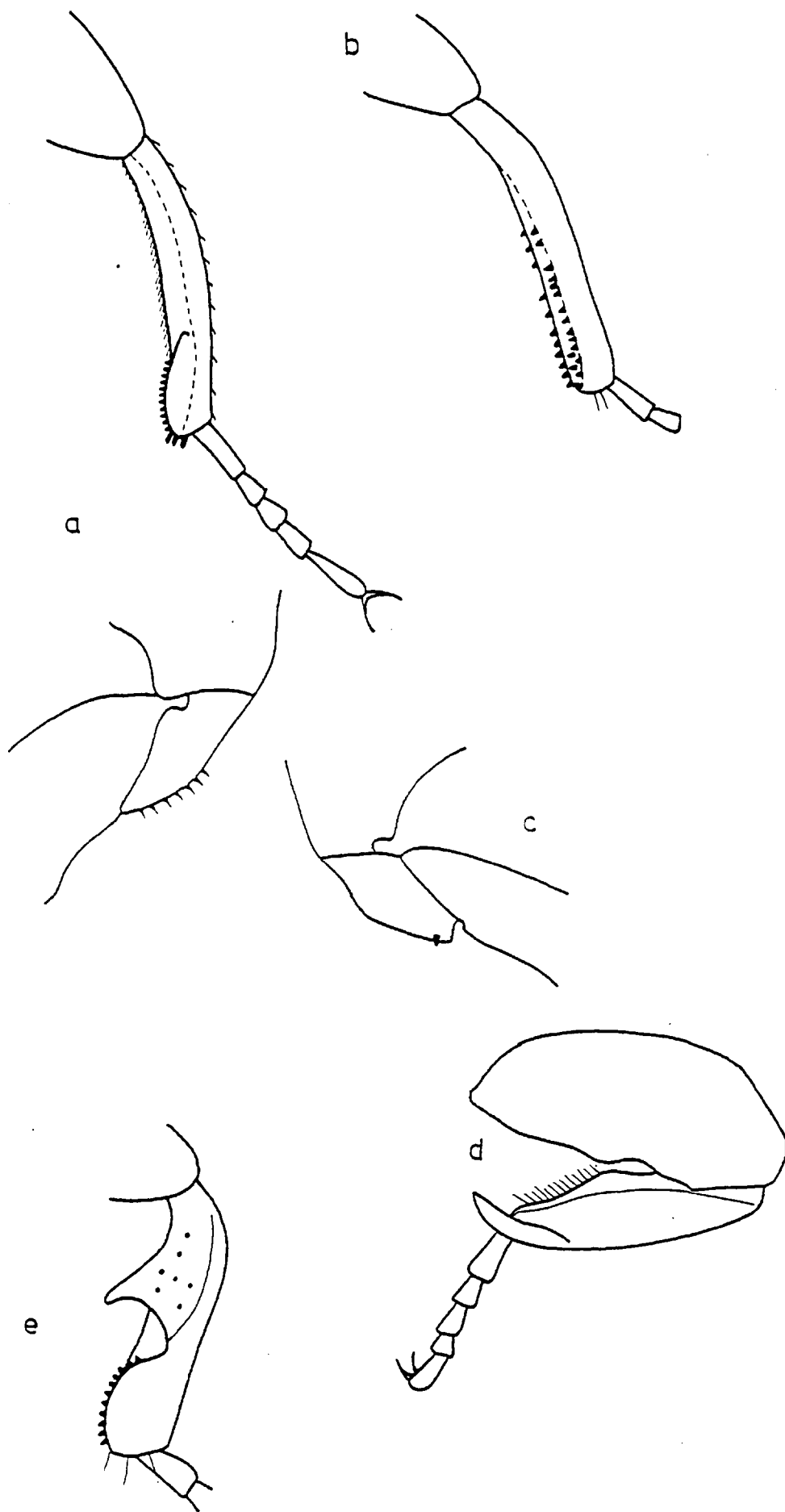


Fig.4.2 Male meta-thoracic legs of Megarathrus, bearing peg setae on the trochanter and tibia, the tibia being sometimes modified in shape, a) M.depressus, b) M.sinuatocollis, c) M.affinis, d) M.denticollis e) M.hemipterus.



0.2mm

elytral apices which are elongate in females, and truncate in males. The elytra are also modified in termitophilous and myrmecophilous aleocharines e.g. Zyras (Tottenham, 1955b).

4.2.3 Abdomen

Owing to the variety of abdominal secondary sexual features they will be further categorised into their different types.

1) Ventral Features

a) Emargination and lobing of sclerites.

Commonly the only abdominal secondary sexual feature in males of a number of staphylinid groups including the Staphylininae, Steninae and Bolitobiini, is the central U or V shaped invagination of the posterior border of the eighth sternite, (Plates 4.1-4.2) e.g. Philonthus, Quedius, Staphylinus, Gabrius. This is associated with the extrusion of the genitalia and the ventrally curved position of the male abdomen during mating. This feature is absent in the Aleocharinae where the male curves the abdomen dorsally during mating. Other sternites, e.g. VI and VII, may also exhibit simple emargination in some groups. More striking modifications of the abdominal sclerites are present in other subfamilies. Three closely related sympatric species of Platystethus (Oxytelinae), (P. cornutus (Grav.), P. degener Muls. & Rey and P. alutaceus Thoms.), and other species groups, have distinct characters of the posterior border of the seventh sternite (Fig. 4.18). Sternite VIII is similarly modified in all members of the subgenus Creatopycrus and there are varied modifications in other sub genera (Hammond, 1972a). In the Steninae, where the secondary sexual characters are generally poor, the Stenus providus group is exceptional in having species, such as S. providus, and S. clavicornis which are broadly sympatric and closely related, exhibiting abdominal differences, although slight (Fig. 4.3).

In the Paederinae abdominal modification in the males is common in Lithocharis, Medon, Scopaeus and other genera. Less common are

Plate.4.1. Scanning electron micrographs of the abdominal segments of
Philonthus sordidus.

- a) Male abdominal sternites VIII, IX and genitalia (x 30)
- b) Female abdominal sternites VIII and IX (x 60)
- c) Male abdominal sternites VI, VII and VIII (x 30)
- d) Female, postero-ventral view sternites VIII and IX (x 72)
- e) Male, postero-ventral view sternites VII, VIII and IX
(x 39)
- f) Female, postero-ventral view valvulae (x 300)

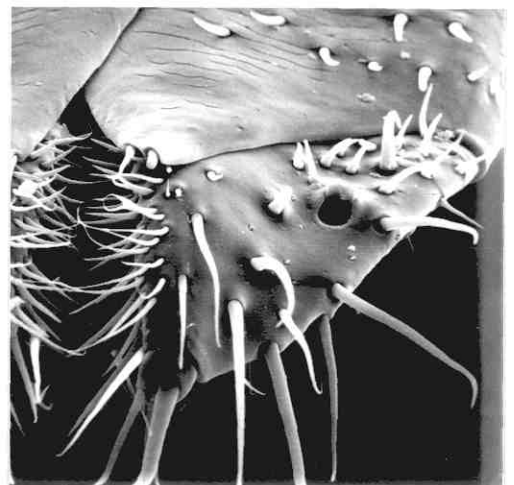
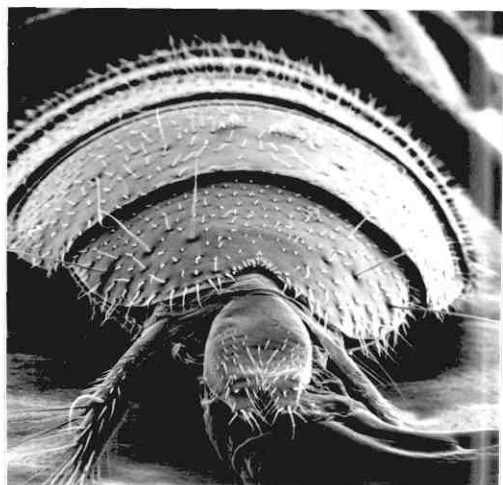
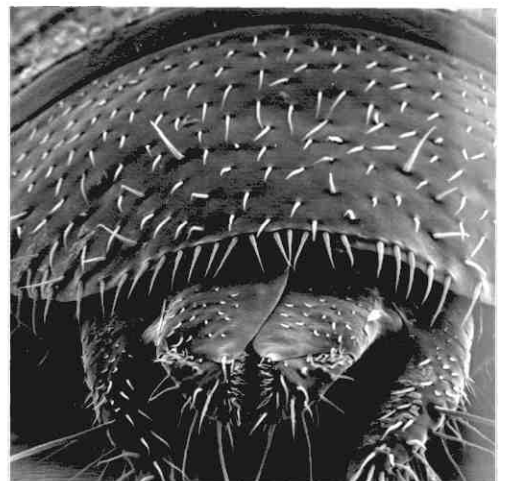
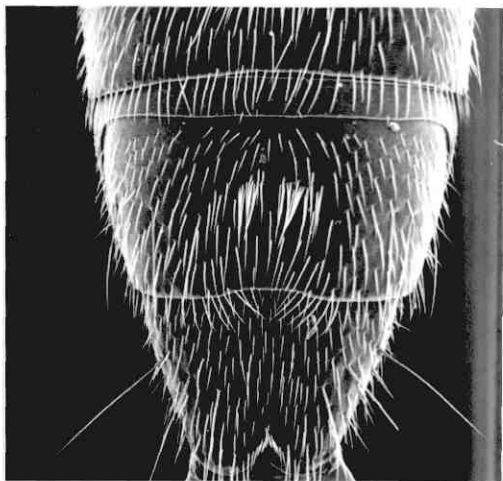
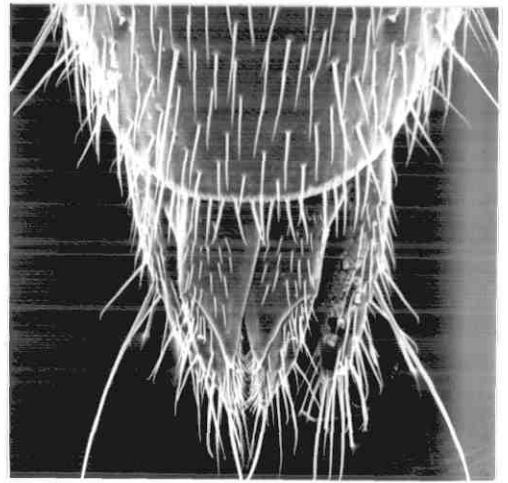
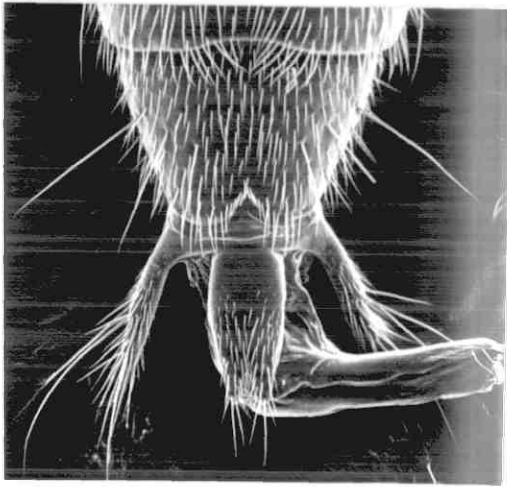


Plate.4.2. Scanning electron micrographs of the abdominal segments of
Philonthus sordidus.

- a) Female abdominal tergites VIII and IX (x 90)
- b) Female, postero-dorsal view tergites VIII and IX (x 90)
- c) Female abdominal tergite VIII (x 108)
- d) Female, postero-dorsal view tergites VII, VIII and IX (x 61)

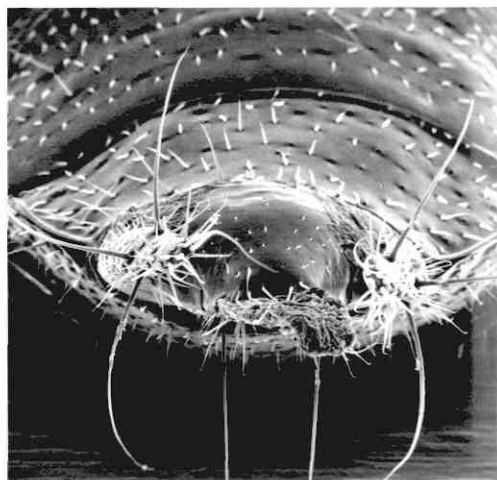
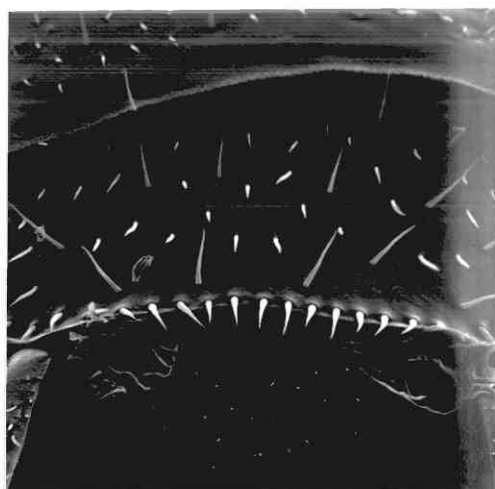
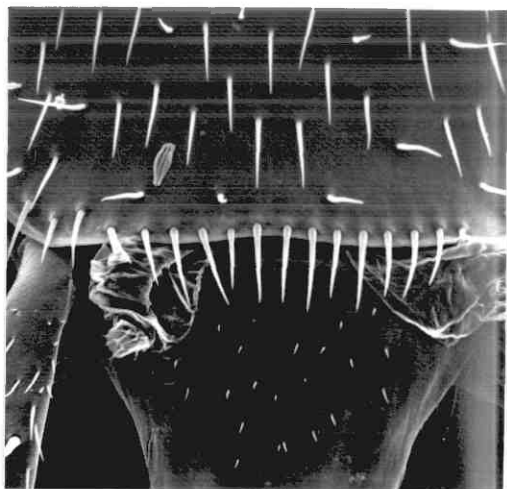
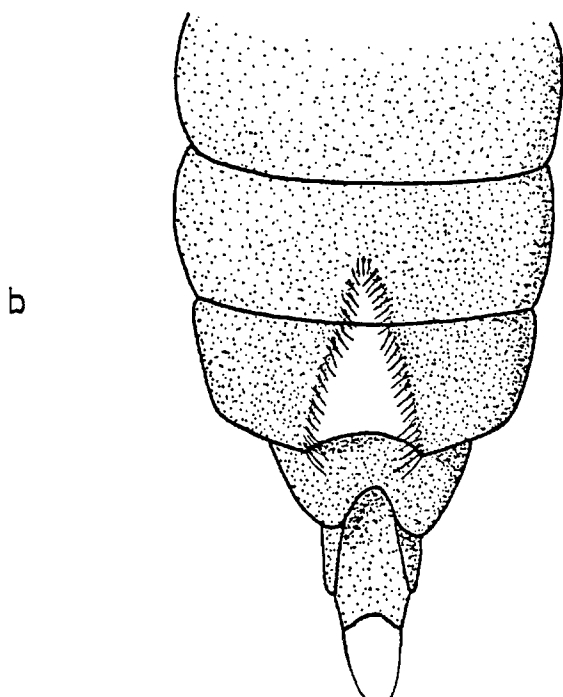
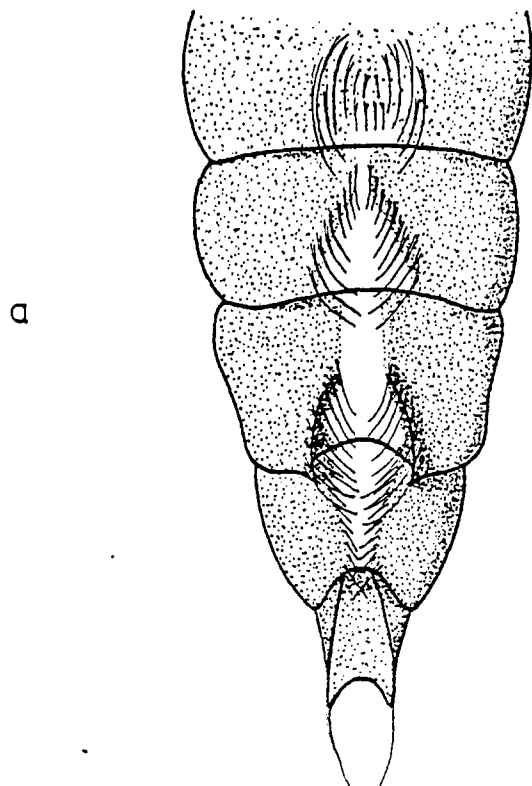


Fig.4.3 Male abdominal segments of Stenus; ventral view,
a) S.providus, b) S.clavicornis.



0.5mm

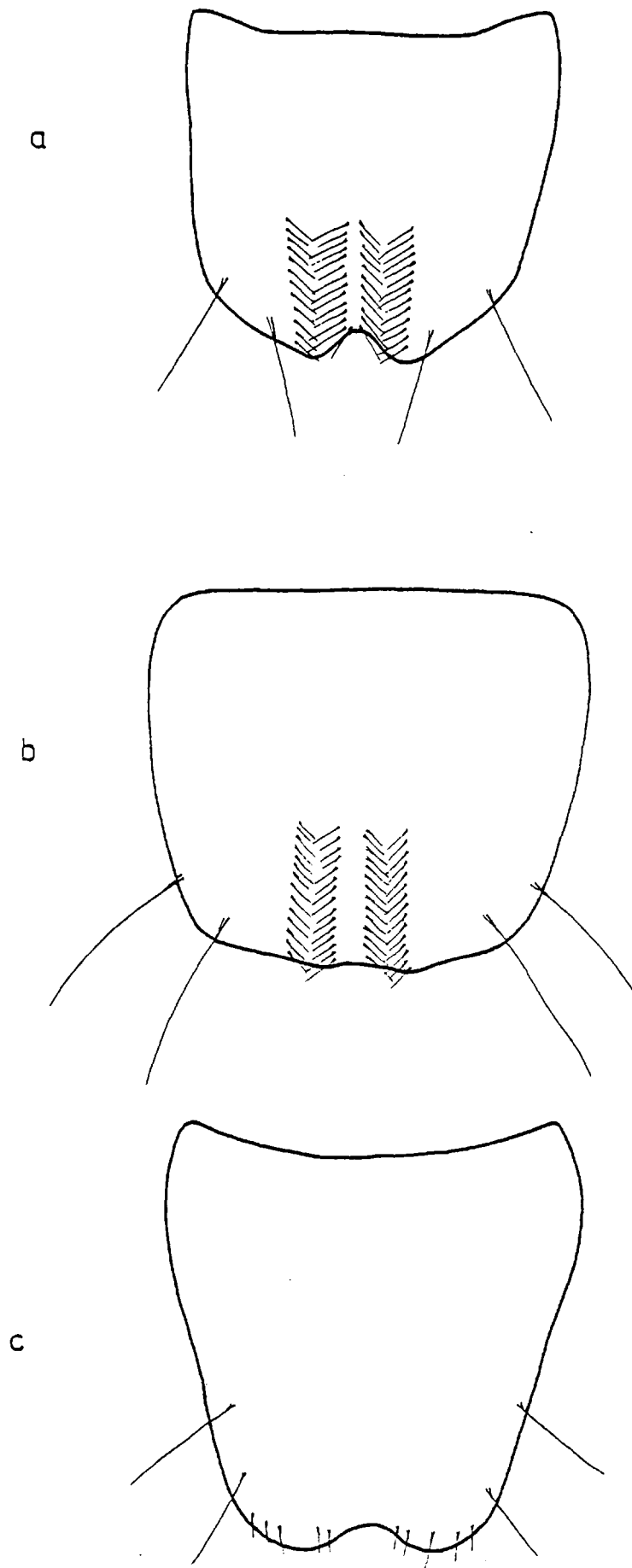
the features exhibited by sympatric species of Lathrobium, (e.g. L. elongatum L., L. fulvipenne Grav., and L. geminum Kr.) where the posterior border of the male eighth sternite is distinctly emarginated (Fig. 4.4). In Lithocharis, Cryptobium, Scopaeus, Medon and Indian Lathrobium, where there is cohabitation of closely related species, there are striking modifications of the male seventh and eighth sternites, each species being quite distinct (Cameron, 1931).

The Tachyporinae exhibit some of the most striking abdominal characters, lobing of sclerites often being accompanied by groups of filiform or peg setae. Mycetoporus splendidus (Grav.), M. longicornis (Maklin) and many related species, exhibit specific modification of the posterior borders of the sixth and seventh sternites (Figs. 4.57-4.58). Similarly in Bolitobius analis (F.) and B. cingulatus (Mann.), the male seventh sternite is a distinct specific character (Fig. 4.60). In Tachinus, both sexes have very striking abdominal secondary sexual characters, the inter-specific differences being diagnostic in many instances. In the male this includes the seventh and eighth sternite and in the female the eighth sternite.

b) Occurrence of patches of pubescence and bundles of setae.

The occurrence of groups of setae is often associated with the lobing or emargination of those sclerites on which they are present. This is the case with Stenus, Lathrobium, Lithocharis, Medon and Bolitobius which have already been mentioned in the previous section. In Stenus providus and S. clavicornis there is a dense pubescence around a glabrous region towards the central posterior border of each sternite from the fifth to the eighth segment. The two species differ in the density of the pubescence and in the length of the setae (Fig. 4.3). Lathrobium elongatum and L. geminum have a similar arrangement of setae associated with the lobes on the posterior border of the male eighth sternite (Fig. 4.4). In Lithocharis and Medon the seventh and sometimes eighth sternites, in the male, have specific arrangements of

Fig.4.4 Male abdominal sternite VIII of Lathrobium, a) L.elongatum ,
b) L.geminum, c) L.fulvipenne.



0.5mm

long setae at their posterior borders (Figs. 4.21-4.26).

c) Occurrence of patches of peg setae.

Modified or peg-like setae may also occur in association with lobing of specific sclerites. The number and precise siting of peg setae is distinct in individual species, and the difference between species often particularly exaggerated when they are closely related and sympatric. Abdominal peg setae have been searched for in the Staphylinidae by Hammond (1972a) where a more complete list of principal sites can be found. One small group of species of Platystethus (Oxytelinae) possess a single peg setae, of characteristic size and shape for each species, on the male eighth sternite. Aploderus spp. (Oxytelinae) bear modified setae on the male sternite VIII. Phloeocharis spp., Derops spp., and Rimulinicola spp., provisionally referred to as the Phloeocharinae by Herman (1972), bear peg setae in groups on the male seventh sternite. Setae, which may be of the peg seta type, are thought to be present on abdominal sternites of some Eutyphlus spp. (Leptotyphlinae). Patches of peg setae occur on the male seventh sternite in Tachinus as well as elongate tapering setae of similar type at the posterior margin of the male seventh sternite and lobes of the female eighth sternite.

d) Occurrence of combs of robust setae.

In the Paederinae peg setae commonly arranged as a comb of flattened and blunt setae are found in certain genera on the posterior margin of the male eighth sternite e.g. Lathrobium, (some species), Lithocharis (including L. ochracea (Grav.) and L. nigriceps Kr. (Figs. 4.22-4.23), Medon, (Fig. 4.21) Astenus and Stilicopsis. In the Tachyporinae combs of a similar type are found in male Tachinoderus, Olophrinus, and Conosomus.

e) Elaborate development of the abdominal sternites (i.e. angled projections, knobs, prongs).

In the genus Anotylus (Oxytelinae), the value of male secondary

sexual features for species discrimination is particularly variable. Male abdominal structure varies little in a number of species groups, and even in some instances where conspicuous modifications are exhibited, inter-specific differences may be small and comparative. Species groups in which diagnostic male secondary sexual features are generally lacking may include a few, generally sympatric species, which exhibit pronounced species specific modifications, (Hammond, 1976). This is the case with A. mutator (Lohse), A. sculpturatus (Grav.) and A. inustus (Grav.) (Hammond, 1968) where the male seventh sternite bears two tubercles near the posterior margin. The position and size of the tubercles, with their associated pubescence, are distinct in each species. The posterior border of the eighth sternite is less different but still specifically distinct. (Fig. 4.20). In the Oxytelinae sternite VIII may have fancy modifications, especially in Oxytelus, and, while also modified, sternite VII is more simple.

In a few groups male abdominal modifications, differing markedly between closely related species, are of more or less general occurrence. This is the case with some Anotylus species e.g. A. fairmairei Pand. (Freude, Harde & Lohse, 1964) where modifications of the sixth sternite are also involved.

f) Extravagant development of the apical segments

In the Staphylininae some Plociopterus spp. possess branched outgrowths of the valvulae of the genital segment. These are highly elaborate and characteristic for each species, and bear patches or rows of peg setae. In addition, combs of long asymmetrical peg setae, stout black tapering setae and bunches of long pale tapering setae occur (Hammond, 1972a).

2) Dorsal Features

Dorsal features are generally confined to those species in which the male mating position involves flexing the abdomen dorsally over

the head, whereby features on the dorsal apical sclerites would make contact with the dorsal apex of the female abdomen. The exception is found in Tachinus spp. where there is marked sexual dimorphism in the tergites of the eighth segment. The male eighth tergite is the least interspecifically variable sclerite; however, intraspecific variation in this segment is known to be quite marked. It is therefore unlikely that these features are utilised in the same way as those involved in tactile recognition.

The Aleocharinae are the principal bearers of dorsal features and this is correlated with the dorsal mating position. There are numerous examples which can be quoted; Gyrophæna is used to illustrate the types of features which occur. In G. pulchella Heer and related species the male eighth tergite has its posterior border distinctly lobed, with the surface of the seventh and eighth tergites bearing raised protuberances (Fig. 4.72).

4.2.4 Genitalia

There are three areas of importance, to be considered here; (i) the shape and chitinous modification of the apex of the median lobe, (ii) the shape and structure of the lateral lobe and (iii) the armature of the internal sac. These are surveyed in a number of the major staphylinid sub-families.

Proteininae

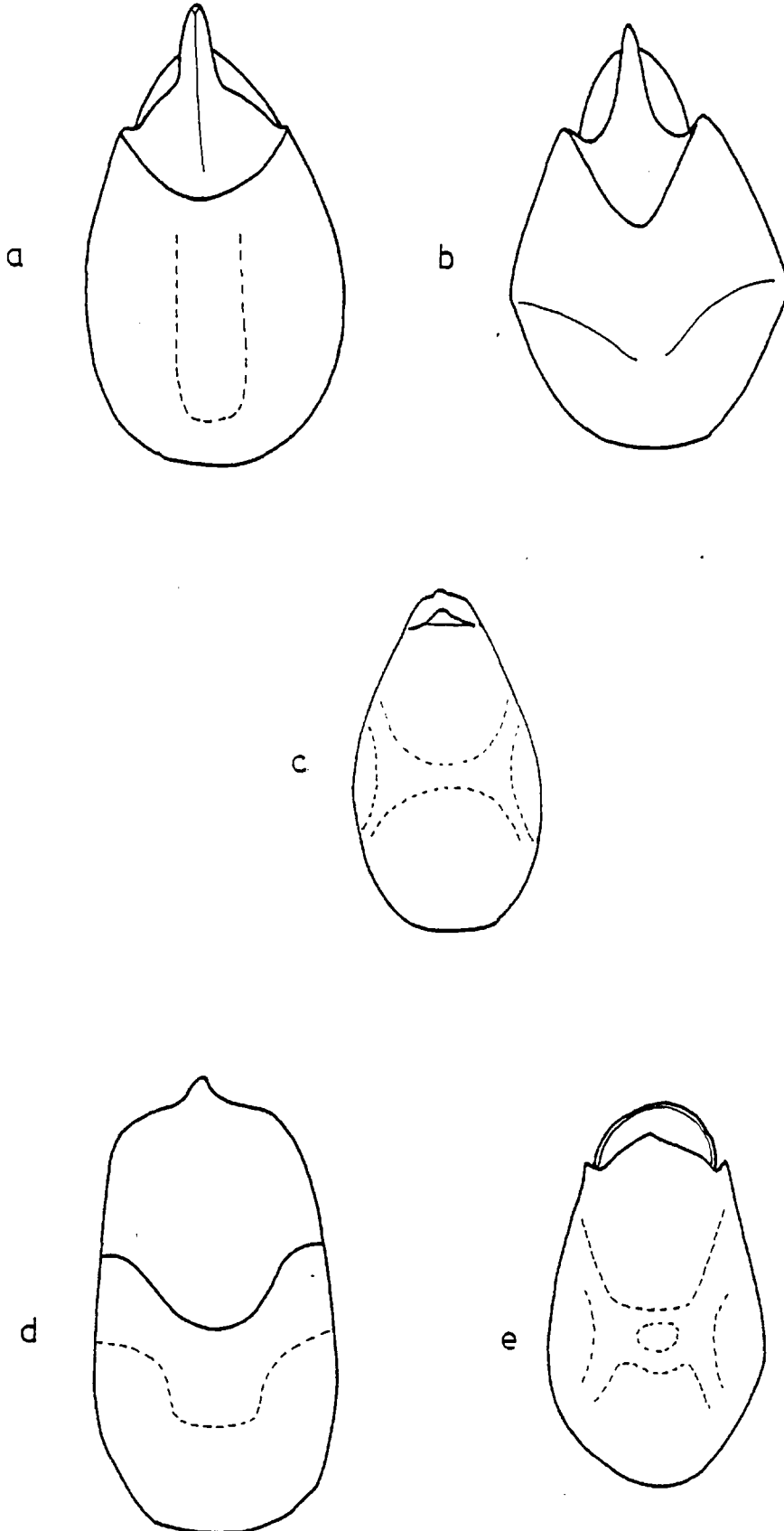
The genitalia generally consist of a single lobe (median lobe) the apex of which may show clear differences between individual species e.g. Megarthus (Fig. 4.5) and Proteinus (Fig. 4.10).

Omaliinae

Omaliine genitalia consist of a median lobe with two lateral lobes. Most of the differences between individual species are comparative, rarely with exaggerated differences between closely related species.

Paraphloeostiba, Phloeonomus, Xylostiba and Eusphalerum, all species of which are associated with sap, rotting fruit or flowers as

Fig.4.5 Male genitalia of Megarathrus, a) M.depressus, b) M.sinuatocollis,
c) M.affinis, d) M.hemipterus, e) M.denticollis.



0.2mm

adults, show relatively large interspecific differences in the structure of the median lobe.

Steel (1960) discusses a departure from the most usual type of genitalia of some species of Paraphloeostiba. This may be seen as a response to selection pressure for assortative mating in sympatric species. However even here such differences are dubious and the distributional data of the species is very limited.

Oxytelinae

Oxyteline genitalia consist of a median lobe with two lateral lobes. In some genera the differences between individual species are comparative e.g. Platystethus comatus, (Fig. 4.17), however, in others there are striking differences in the structure of the lateral lobes and less often in the apex of the median lobe, e.g. Thinobius praetor Smet. and T. crinifer Smet. and T. strandi Smet. (Fig. 4.6) (Smetana, 1959, 1960). In Carpelimus corticinus and C. subtilicornis, which are sympatric in the broad sense but rarely cohabit, substantial differences are apparent in the lateral lobes (Fig. 4.7) (Steel, 1956). However, the lateral lobes are not strongly chitinated and so the differences may not be of significance in tactile recognition. The armature of the internal sac is also strikingly different in these two species of Carpelimus.

In Anotylus the form of the median lobe generally differs little between closely related species; however, the lateral lobes may be strikingly different (e.g. Anotylus sculpturatus and A. mutator, Fig. 4.20). Other species of the same group exhibit little modification, the lateral lobes being of simple form. Lateral lobes are strikingly different in some species of Oxytelus, including some asymmetry in Anotylus fairmairei and related species (Freude, Harde & Lohse, 1964).

Fig.4.6 Male genitalia of Thinobius (after Smetana,1959), a) T.praetor i.ventral view ii. lateral view, b) T.crinifer i.ventral view ii.dorsal view, c) T.strandi i.ventral view ii.dorsal view.

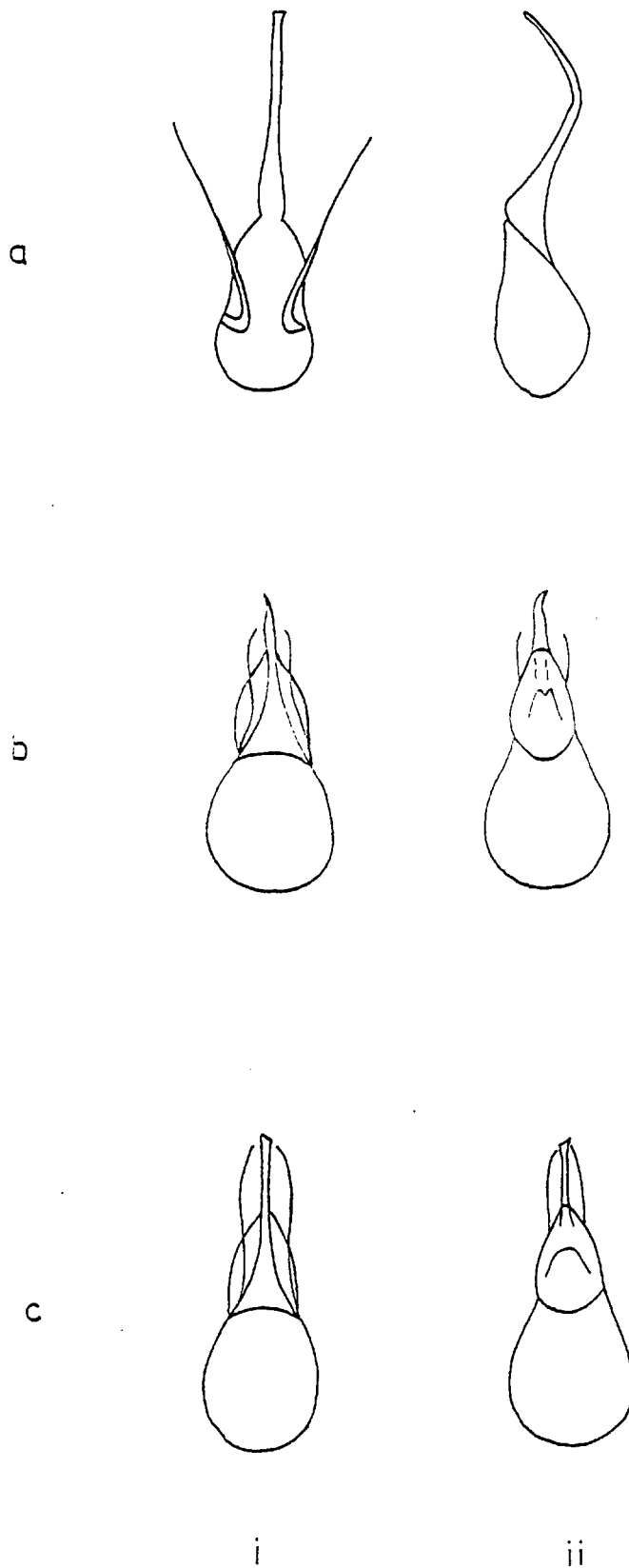
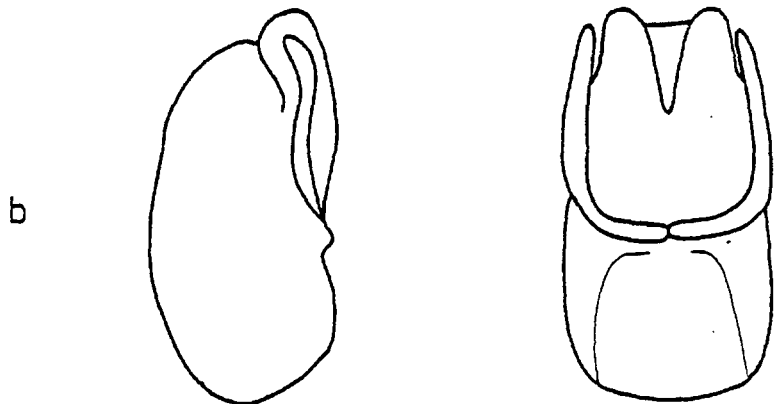
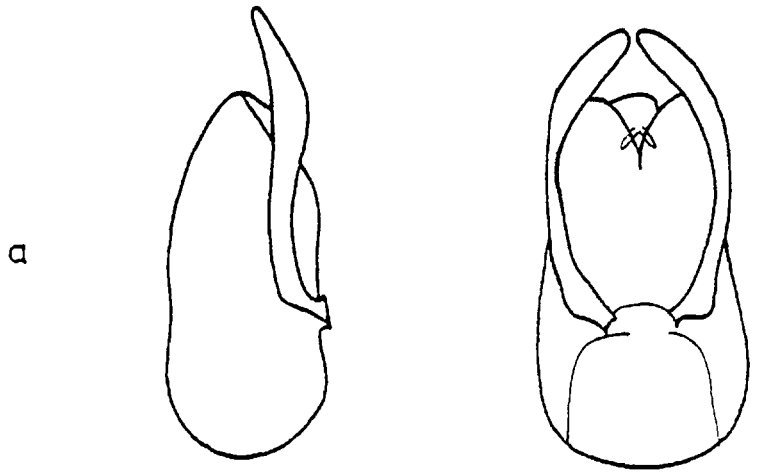


Fig.4.7 Male genitalia of Carpelimus (after Steel,1956),

a) C.subtillicornis i.lateral view ii.dorsal view

b) C.corticinus i.lateral view ii.dorsal view



i

ii

Steninae

The genitalia consist of a median lobe and two lateral lobes. The differences in genitalia are not extreme and are sometimes restricted to the internal sac. The lateral lobes of some closely related species of "Hemistenus" and "Hypostenus" are often strikingly different (Puthz, 1965; and Tottenham, 1948), also S. providus and S. clavicornis (Fig. 4.8). Generally, however, the differences are not exaggerated between closely related species (Puthz, 1971).

Paederinae

Paederine genitalia consist of a median lobe with two separate or fused lateral lobes. Sometimes the lateral lobes are absent. Marked differences in the genitalia, notably of the median lobe apex, are common in the paederines. Examples include three morphologically very similar species of Lathrobium which are sympatric, (L. elongatum, L. fulvipenne and L. geminum) and have very different genitalia (Fig. 4.9). Lithocharis nigriceps and L. ochracea (Fig. 4.22) are sympatric with markedly different genitalia, and likewise the genera Medon and Scopaeus have closely related sympatric species with elaborate genitalia the apical portions of which differ considerably between individual species (Fig. 4.21).

Staphylininae

Different tribes in this sub-family vary in respect of the genitalia. (Section 7). In the Xantholinini and the Othiini, the median lobe is large, dorso-ventrally flattened and may have two small lateral lobes. Differences in male secondary sexual features are largely restricted to the elaborate armature of the internal sac.

In the Staphylinini there is a median lobe with two separate or fused lateral lobes; both types provide a wealth of secondary sexual characters. Differences in these features are often exaggerated between closely related sympatric species. Structures of importance include the apex of the median lobe, the shape, size and structure of

Fig.4.8 Male genitalia of Stenus, a) S.providus i.ventral view
ii. dorsal view, b) S.clavicornis i.ventral view ii. dorsal view.

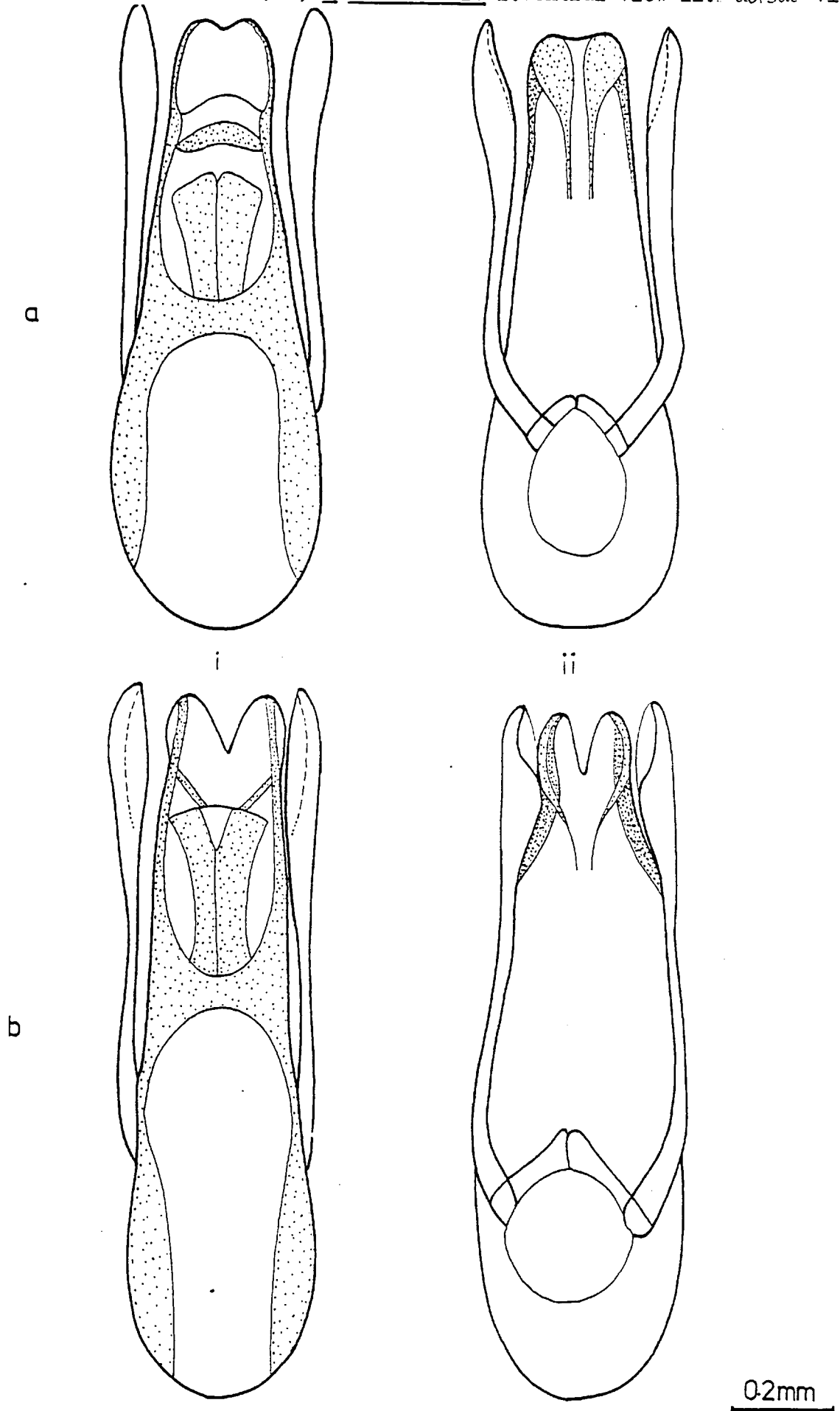
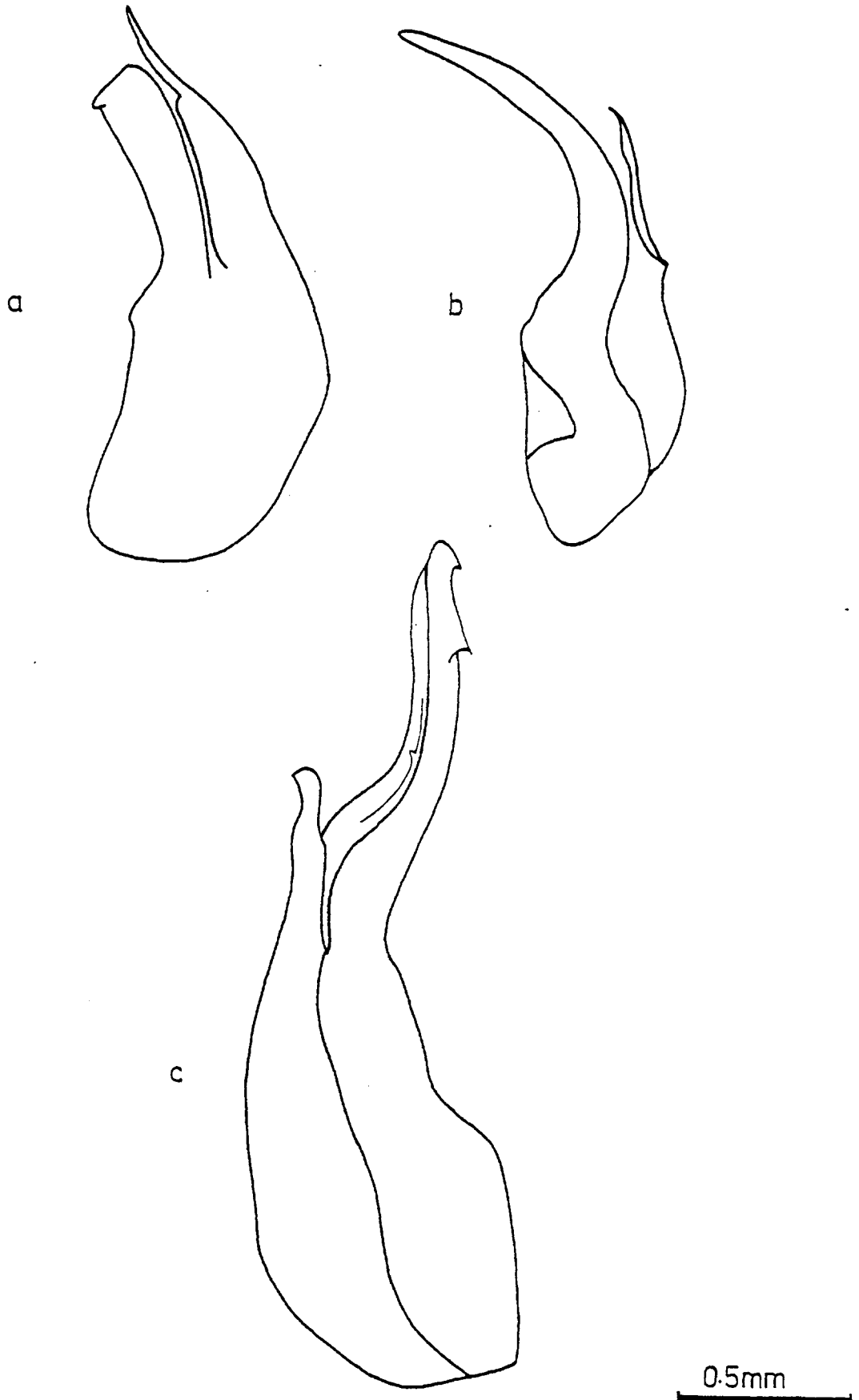


Fig.4.9 Male genitalia of Lathrobium, a) L.elongatum, b) L.fulvipenne,
c) L.geminum.



the lateral lobe/s and the armature of the internal sac. Many staphylinine species bear peg setae on the internal surface of the lateral lobe/s. The number and distribution of pegs is characteristic for a species with greater differences between closely related sympatric species (e.g. Quedius mesomelinus Marsh. and Q. maurus Sahlb. (Section 6.)

Tachyporinae

The genitalia consist of a median lobe with two lateral lobes which are often more or less fused to the median lobe. Generally the genitalia do not possess striking secondary sexual features and differences between species are comparative e.g. Mycetoporus longicornis and M. splendidus (Figs. 4.57 & 4.58) and Tachinus. Bolitobius analis and B. cingulatus exhibit slightly greater differences in apical structures (Fig. 4.61). Larger interspecific differences are most often restricted to the internal sac and its armature.

Aleocharinae

The genitalia consist of a median lobe and two distinctive lateral lobes which are large, composed of three sclerites and have chitinated ribs. Differences between closely related species in lateral lobe structure is slight (Welch, 1964; Seevers, 1978; and Klimaszewski, 1979). There is considerable diversity in the structure of the median lobe apex and this is used as a specific diagnostic feature, e.g. Gyrophana, Cypha, Atheta (Philhygra). In many cases, like the Tachyporinae, marked interspecific differences are again restricted to the internal sac and its armature.

Marked interspecific differences in structure of the well sclerotised female spermothea is also typical of many aleocharines (Seevers, 1978; and Freude, Harde & Lohse, 1974).

4.3. Examination of closely related species pairs/groups.

The major subfamilies are treated in turn.

4.3.1 Proteininae

Proteinus LatreilleP. atomarius ErichsonP. brachypterus (Fabricus)P. crenulatus Pandelle'P. macropterus (Gravenhorst)P. ovalis StephensDistribution and Habitat

All five species are broadly sympatric. Detailed distribution is given by Hammond (in press).

P. atomarius

Northern Europe, from the British Isles east to Caucasus (including all the Scandinavian countries, France, Germany, Austria, Switzerland, Czechoslovakia, Poland).

P. brachypterus

Western Palaearctic region, including France, Spain, Algeria, Poland, Czechoslovakia, Hungary, Yugoslavia, Roumania, Greece, south Russia.

P. crenulatus

Northern Europe to Caucasus and western Siberia.

P. macropterus

West and central Europe (including France, Germany, Poland, Czechoslovakia, Hungary, and all the Scandinavian countries).

P. ovalis

Western Palaearctic, (including France, Spain, Germany, Czechoslovakia, Turkey, Lebanon, south Russia; not known from Scandinavia).

The British distribution of these species is very similar. However, the distribution of P. crenulatus is uncertain although there are specimens from Shropshire, Derbyshire, Nottinghamshire, Cheshire,

Cumberland, north Wales and Scotland in the BMNH. P. atomarius is a woodland species and is found in fresh and rotting fungi, and also in carrion and dung. P. brachypterus and P. crenulatus occur mostly in rotting fungi, but also in decaying leaves, hay or straw, dung, compost, moss and carrion. P. ovalis occurs in more synanthropic habitats, but also in rotting matter including fungi and also dung, carrion, litter in coniferous forests.

P. atomarius, P. brachypterus, P. crenulatus and P. ovalis can be found together. However, P. atomarius is more likely to be found with P. brachypterus, P. crenulatus with P. brachypterus, and P. ovalis with P. brachypterus. P. macropterus has a different habitat and is generally not found together with the other species (Hammond, in press^c).

Secondary Sexual Characters

Male secondary sexual characters involve modification of the mid and hind legs, and the structure of the aedeagus. As with Megarathrus species, the females are without corresponding structures.

P. atomarius

This species is very much smaller than the others in the group.

Legs: unmodified.

Aedeagus: very small and distinct from the other species in apical structure. (Fig. 4.10d).

P. brachypterus

mid-leg: tibia with a row of peg setae along the interior edge, from half-way along its length to the distal end (Fig. 4.11d).

hind-leg: simple, without modification.

aedeagus: very small, apically distinct (Fig. 4.10c).

P. crenulatus

mid-leg: femur with 1-2 short spined setae near to the distal end on the interior surface.

: tibia with a row of peg setae along the interior edge from half-way along its length to the distal end (Fig. 4.11c).

Fig.4.10 Male genitalia of Proteinus, a) P.ovalis i.lateral view
ii.dorsal view, b) P.macropterus lateral view,
c) P.brachypterus lateral view, d) P.atomarius lateral view.

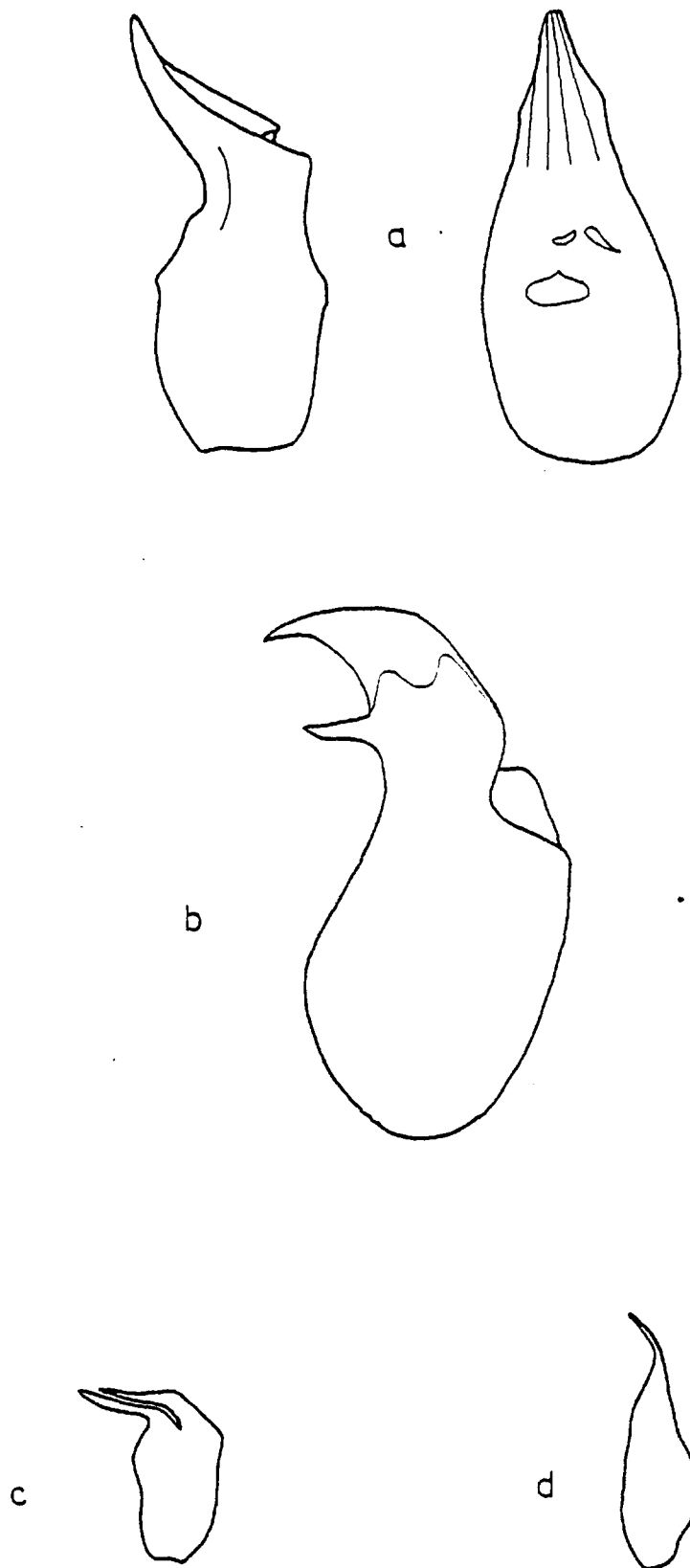


Fig.4.11 Male meso-thoracic legs of Proteinus; inner view,

a) P.ovalis, b) P.macropterus, c) P.crenulatus d) P.brachypterus.

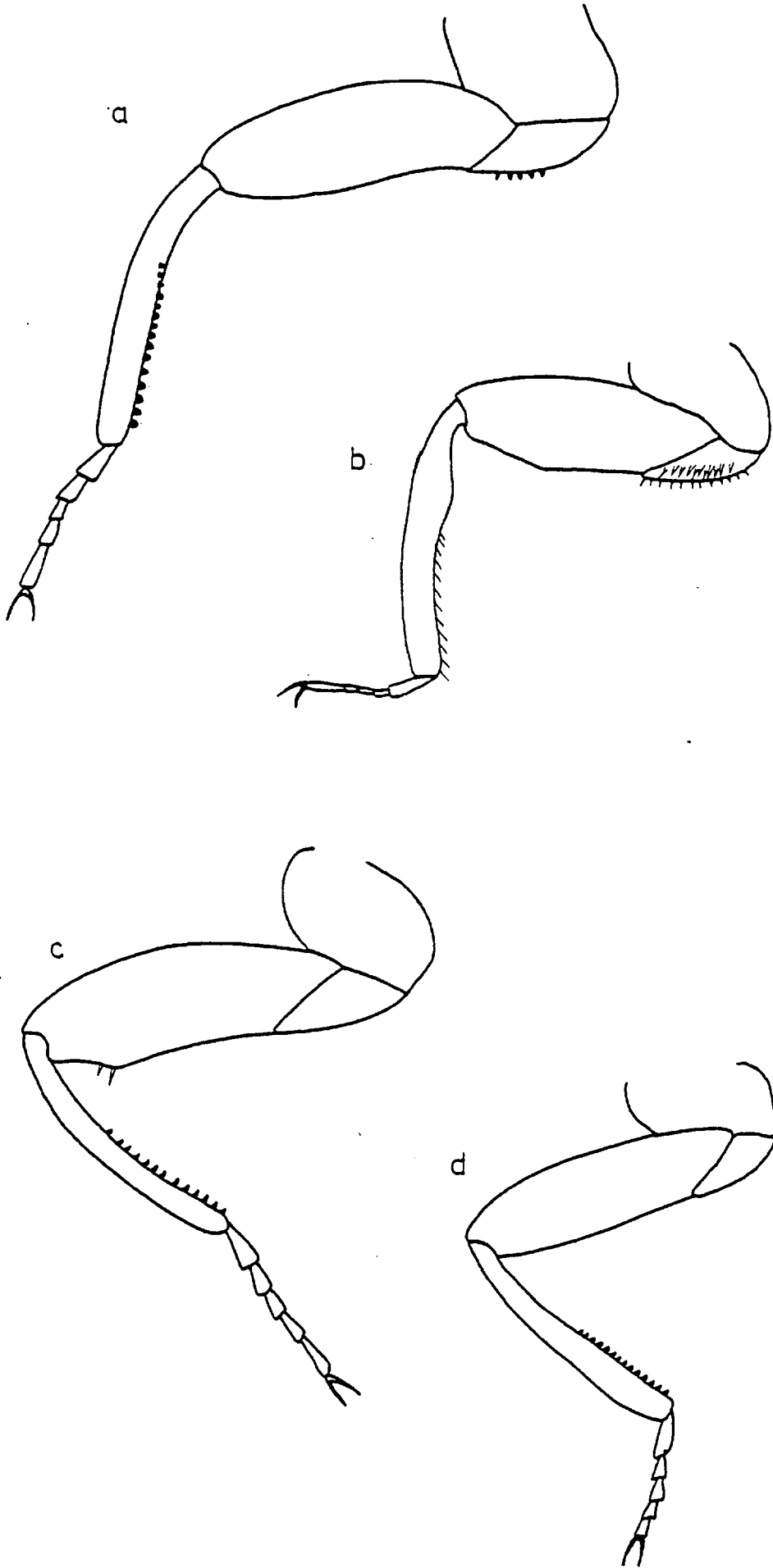
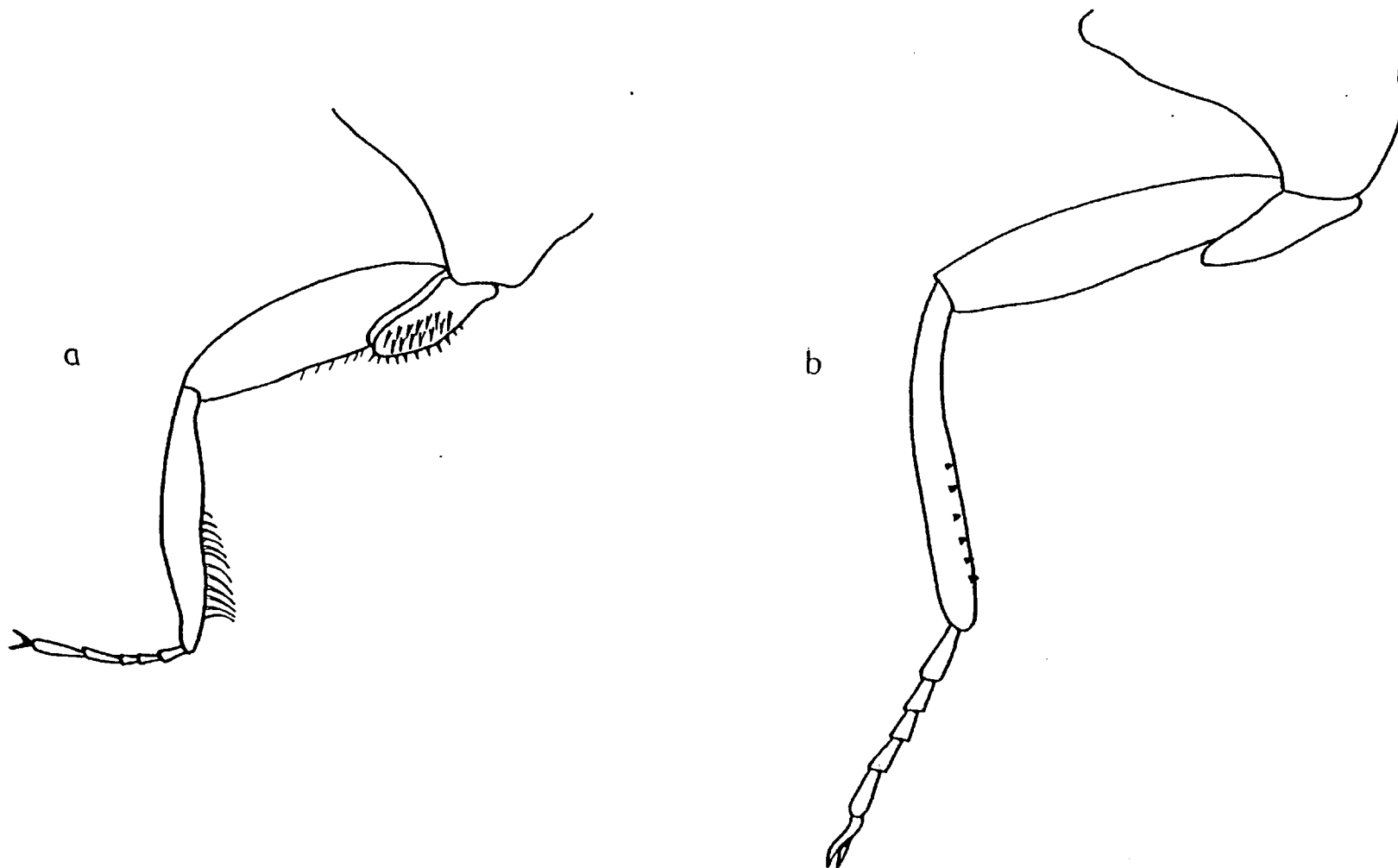


Fig.4.12 Male meta-thoracic legs of Proteinus; inner view, a) P.macropterus, b) P.ovalis.



hind-leg: simple, without modification.

aedeagus: large, apically distinct.

P. macropterus

Exhibits the most distinct secondary sexual characters.

mid-leg: trochanter with spicules over the interior surface
(Fig. 4.11b).

: tibia with row of spicules along the interior edge
from half-way along its length to the distal end (Fig. 4.11b).

hind-leg: trochanter with spicules over the interior surface (Fig. 4.12a).

: femur with spicules along proximal interior edge.

: tibia with a row of spined setae towards the distal end
of the interior edge (Fig. 4.12a).

aedeagus: similar in size to P. crenulatus, apically distinct
(Fig. 4.10b).

P. ovalis

mid-leg: trochanter with about 5 peg setae on the interior edge
(Fig. 4.11a).

: tibia with row of peg setae along the interior edge.

hind-leg: tibia with about 6 peg setae along the interior edge
towards the distal end (Fig. 4.12b).

aedeagus: apically distinct (Fig. 4.10a).

Variation

There is some variation in the number of peg setae within a particular species, however the siting and type of setae is probably more important. This is also the case in species of Megarthus.

The range of variation in Megarthus is illustrated from European and Indian species (Figs. 4.1, 4.2, 4.13 and 4.14).

Function

There is no available information on mating behaviour in the Proteininae, except that it is known that the male mounts the female dorsum. It is most likely that the structures are of use during mating,

Fig.4.13 Male meso and meta-thoracic legs of Indian Megarathrus; ventral view, a) M.alticola meta-thoracic leg, b) M.flavolimbatus meta-thoracic leg, c) M.alticola meso-thoracic leg, d) M.flavolimbatus meso-thoracic leg.

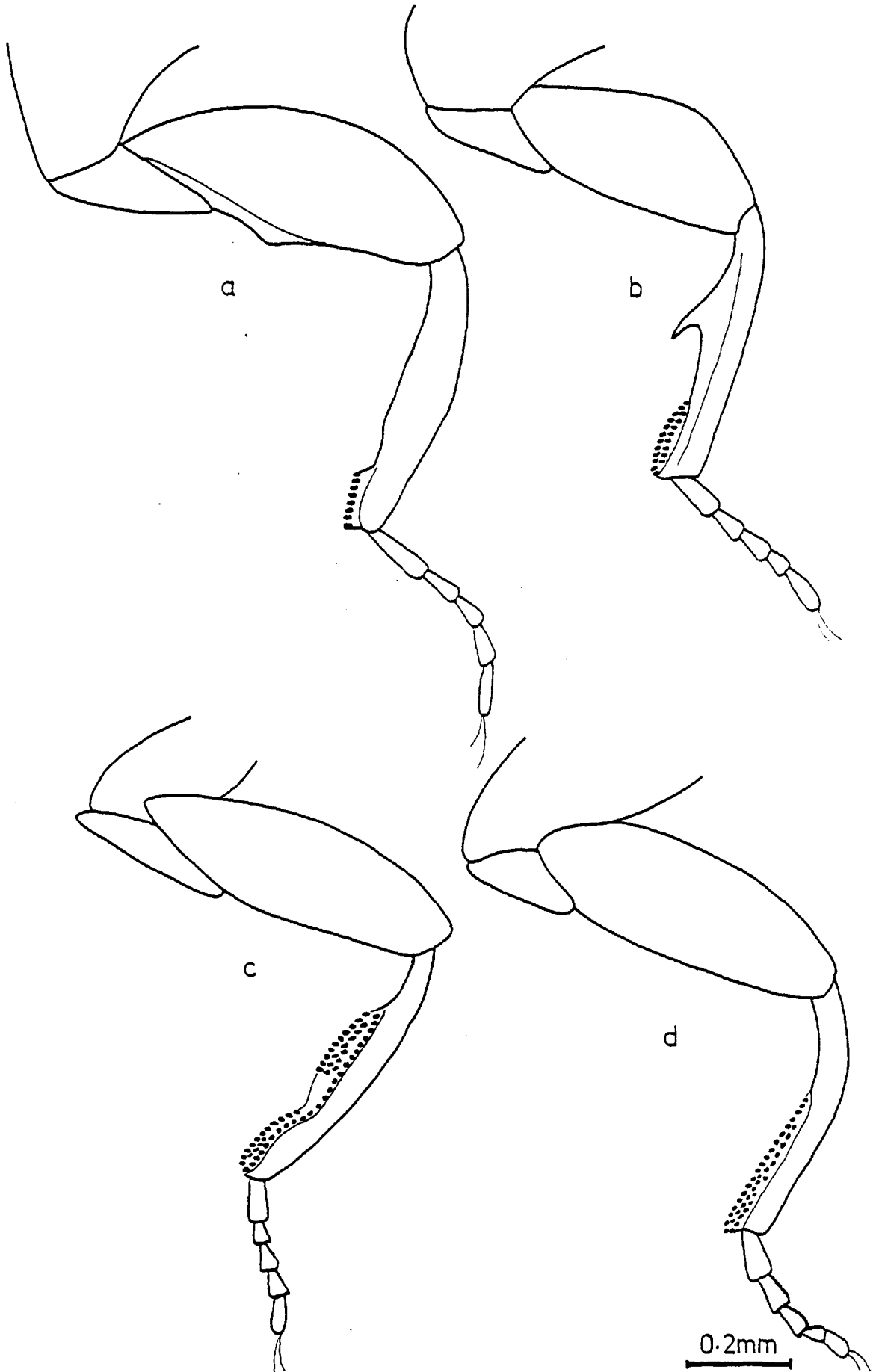
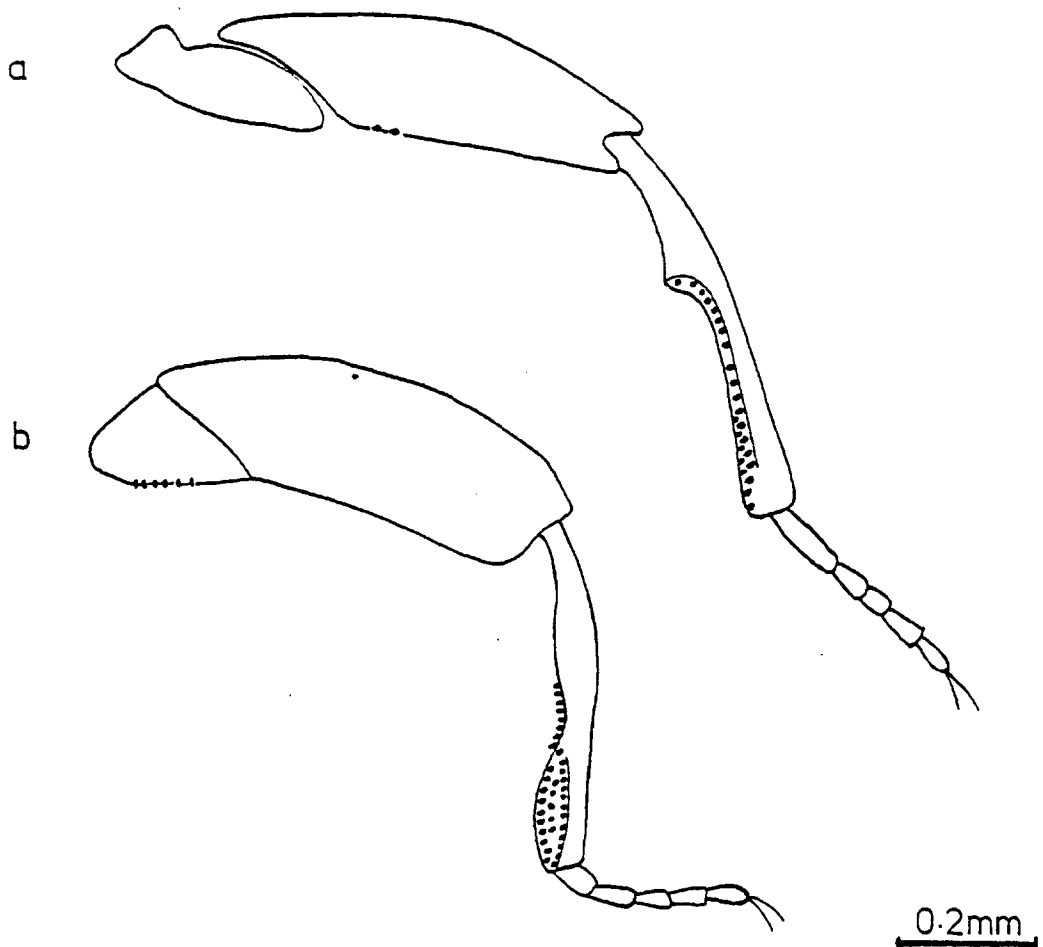


Fig.4.14 Male meso and meta-thoracic legs of Indian Megarathrus ; dorsal view, a) M.nitidulus meta-thoracic leg, b) M.nitidulus meso-thoracic leg.



since they are only present in males. The peg setae and spicules occur on the interior surface of the legs, in a position where they would come into contact with the female abdomen during mating. It is difficult to hypothesise a mechanical function for such structures and owing to the differences between the syntopic species they may be regarded as tactile recognition features.

The British Megarathrus species are not ideal for real comparisons, as their relationships are poorly known.

It is known, however, that M. depressus cohabits with the apparently very closely related M. nitidulus in Europe (but not in Britain) and their secondary sexual features are different (Figs. 4.1, 4.2, 4.13 and 4.14).

4.3.2 Omaliinae

The Omaliinae generally lack pronounced secondary sexual features. Males of closely related species rarely possess highly divergent developments in genital and other characters as has been already mentioned (Section 4.2).

There is some evidence of use of pheromones during courtship in Eusphalerum (Blum, 1976) and Olophrum (Scheerpeltz, 1929). If the pheromones are at all specific their use may be directly related to the absence of other obvious signal characters in closely related species of these genera.

Acrolocha Thomson

A. minuta (Oliver)

A. sulcula (Stephens)

A. minuta and A. sulcula are the British representatives of the genus in which there are six species.

Distribution and Habitat.

The range of the genus includes Europe, western Asia and North America, in fragmented habitats such as fungi, dung and decaying vegetable matter (Steel, 1957).

A. minuta and A. sulcula are broadly sympatric in the western Palaearctic. A. sulcula is widespread over Britain, but A. minuta is known only from the London area and the Sussex coast (BMNH).

A. sulcula is found mostly in dung, but sometimes in compost and rotting vegetation, whereas A. minuta is synanthropic in Britain occurring in compost and similar habitats. The adults of A. sulcula are active from July-October with a peak at September, while A. minuta adults are winter active from October-February; there is some overlap in their activity cycles (Hammond, in press^c).

Secondary Sexual Characters

The main differences between the two species lie in their secondary sexual characters.

A. minuta

Male

Hind leg: posterior trochanters obliquely truncate externally and with the postero-external angle produced into a small outwardly directed tooth. (Fig. 4.15e).

Abdomen: posterior margin of sternite VII very finely denticulate in the middle. (Fig. 4.15c).

Aedeagus: of characteristic form. (Fig. 4.15a).

Female

Hind leg: posterior trochanters unmodified. (Fig. 4.15f).

Abdomen: posterior margin of sternite VII simple.

A. sulcula

Male

Hind leg: posterior margin of sternite VII broadly emarginate with a distinct tooth in the mid-line. (Fig. 4.15d).

Aedeagus: of characteristic form. (Fig. 4.15b).

Phloeonomus Heer

P. punctipennis Thomson

P. pusillus (Grav.)

These two species which are the only two of the genus occurring in Britain were long confused, with P. punctipennis being regarded as a variety of P. pusillus. However, on the basis of genital and other characters it is now established that they are distinct species with minor external differences (Coiffait, 1953).

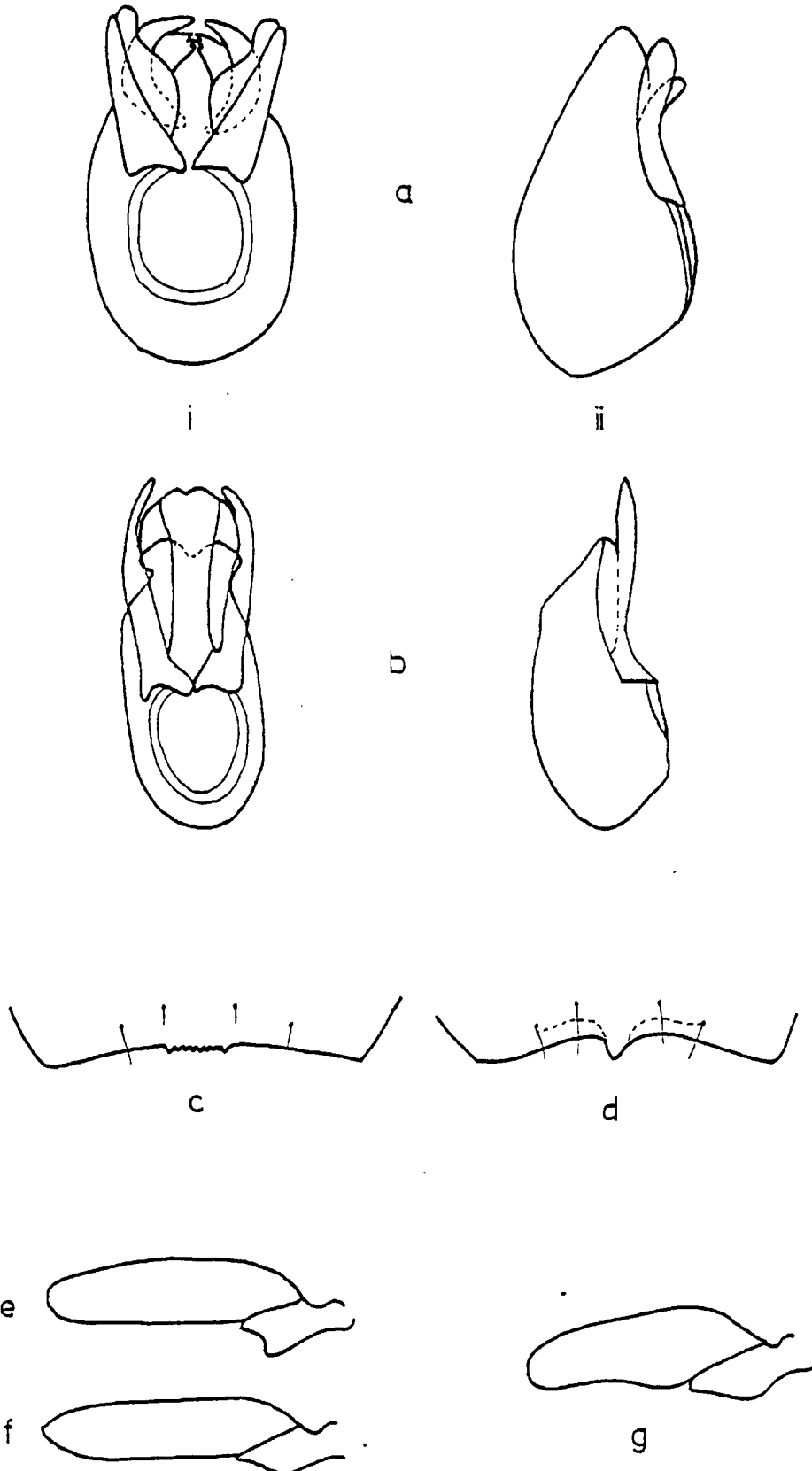
Distribution and HabitatP. punctipennis

Distributed throughout most of Europe, although more seldom in central and southern areas.

P. pusillus

Palearctic and North America. Records of their British

Fig. 4.15 Acrolocha (after Steel, 1957), a) A.minuta ♂ genitalia i.ventral view ii.lateral view, b) A.sulcula ♂ genitalia i.ventral view ii.lateral view, c) A.minuta ♂ sternite VII, d) A.sulcula ♂ sternite VII, e) A.minuta ♂ posterior trochanter, f) A.minuta ♀ posterior trochanter, g) A.sulcula ♂ and ♀ posterior trochanter.



distributions (BMNH) indicate that they are similar and widespread. P. pusillus is found mostly under coniferous wood bark and more seldom under the bark of deciduous trees. In contrast, P. punctipennis is a deciduous wood specialist, found under bark, directly in the sap and in tree fungi. They are however sometimes found syntopically.

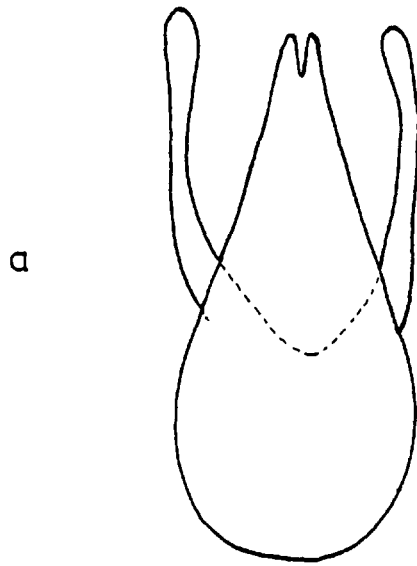
Secondary Sexual Characters

The aedeagus of both species is characteristic and distinct, Fig. 4.16.

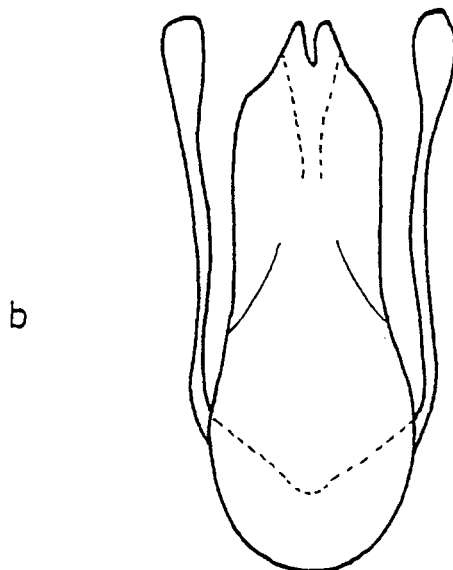
Paraphloeostiba Steel

In this Old World Tropical genus, many species of which are associated with rotting fruit or plant sap, the male genitalia of some species depart from the usual form. Some species are very closely allied and are difficult to separate using external characters. However, the male aedeagus shows appreciable interspecific differences and in the females a structure associated with the ovipositor, of unknown function, is equally valuable. These structures are figured by Steel (1960).

Fig.4.16 Male genitalia of Phloeonomus, a) P.pusillus, b) P.punctipennis.



0.1mm



0.1mm

4.3.3. Oxytelinae.

Mating behaviour in the Oxytelinae has only been recorded in Oxytelus sculptus (Section 5.2.13). The abdominal features, due to their siting and constancy, are of the type that might be used in tactile recognition. Features of the genitalia are unlikely to be involved owing to the small differences between species.

Platystethus. Mannerheim.

<u>P. alutaceus</u>	Thomson
<u>P. cornutus</u>	(Gravenhorst)
<u>P. degener</u>	Mulsant & Rey

Distribution and Habitat

All three species are sympatric. Detailed distribution is given by Horion (1963) and Hammond (1971).

P. alutaceus.

Widespread in central and southern Europe and in the Mediterranean area. Distribution in the east extending at least to Asia Minor, in the north to southern Britain and southern Scandinavia.

P. cornutus

Widespread in the Palaearctic and Oriental regions from Spain to eastern Siberia, Japan and Taiwan in the east, and from England, southern Scandinavia and Siberia south to Morocco, Algeria south India and Vietnam.

P. degener

Generally more southern than P. cornutus although the ranges largely overlap. Few records from north and central Europe but large numbers from the Mediterranean region, Asia Minor, Madeira and the Canaries, also north India but not China or Siberia.

Their British distributions are mapped by Hammond (1971).

P. alutaceus is confined to the southern half of England where it is regarded as local or very local. P. cornutus is probably generally

distributed in southern England with scattered records from Co. Durham, Yorkshire and Lancashire and also southern Scotland and the south of Ireland. The distribution of P. degener in Britain is similar to P. cornutus, but apparently not reaching as far north.

P. cornutus and P. degener burrow in mud on the banks of ponds and rivers or in marshy situations, P. degener having a preference for mud with a high organic content. In Britain P. cornutus seems to be the more generally distributed and abundant of the two, while in southern Europe the position is reversed, although mixed populations are not uncommon. Habitats of P. alutaceus seem to be similar to P. cornutus but it is rarely found with either P. cornutus or with P. degener probably owing to a difference in substrate preference. However, all three species may be taken from a single patch of mud (Hammond, pers. comm).

Secondary Sexual Characters

Although the male secondary sexual characters are minor, constant differences are seen between the three species.

The genitalia exhibit very minor differences, mainly in the shape of the apex of the lateral lobe and its curvature, however there is some geographical variation in these features within each species (Fig. 4.17). More striking differences are present in the posterior border of the male seventh sternite which has two posteriorly directed projections which are separated by a different and constant distance in each species (Fig. 4.18).

Variation

There is little or no intra-specific geographical variation in the features of the seventh sternite.

Anotylus

A. inustus (Gravenhorst)

Fig.4.17 Male genitalia of Platystethus; i. dorsal view ii. lateral view iii. lateral lobe , a) P.alutaceus, b) P.cornutus, c) P.degener.

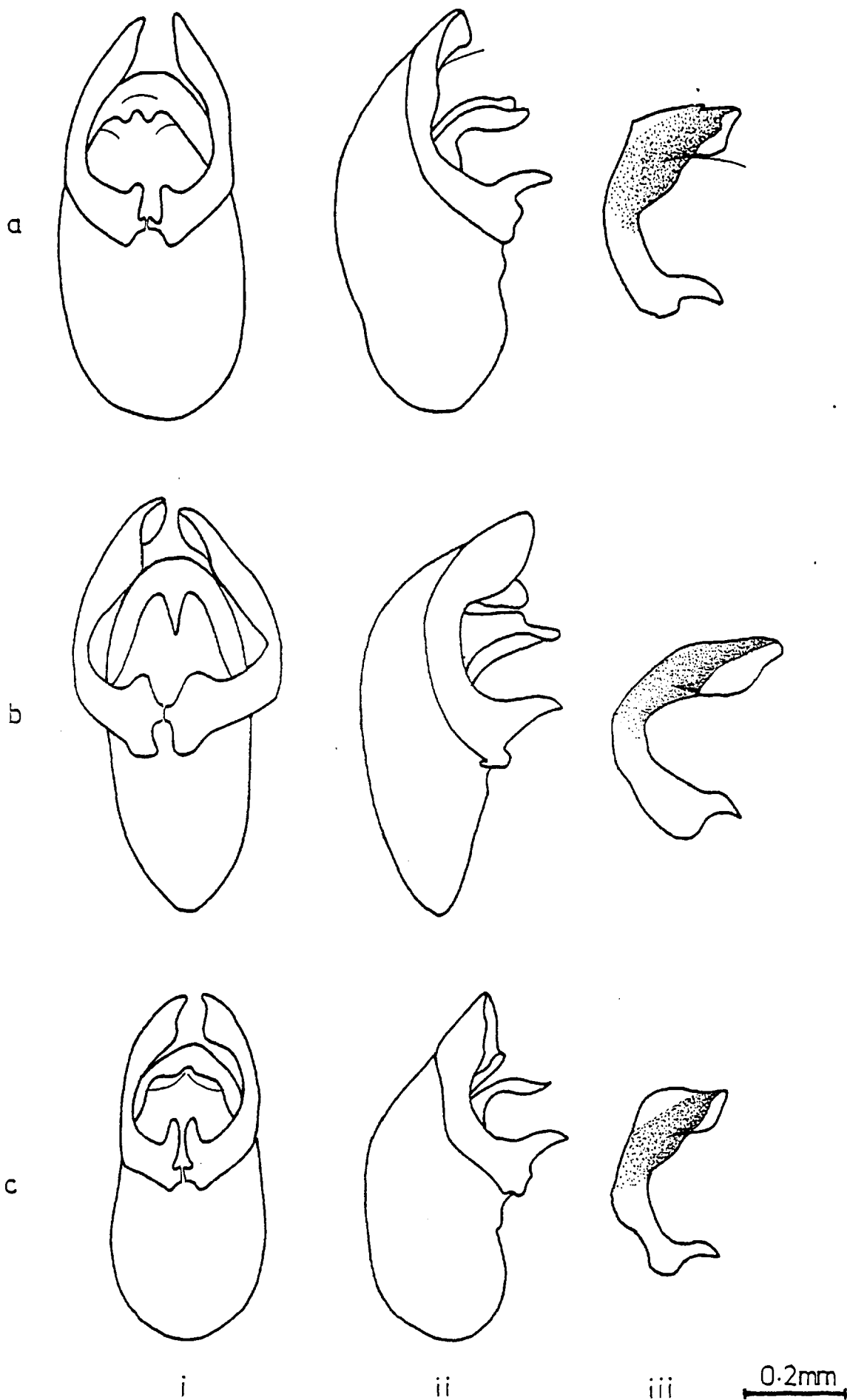
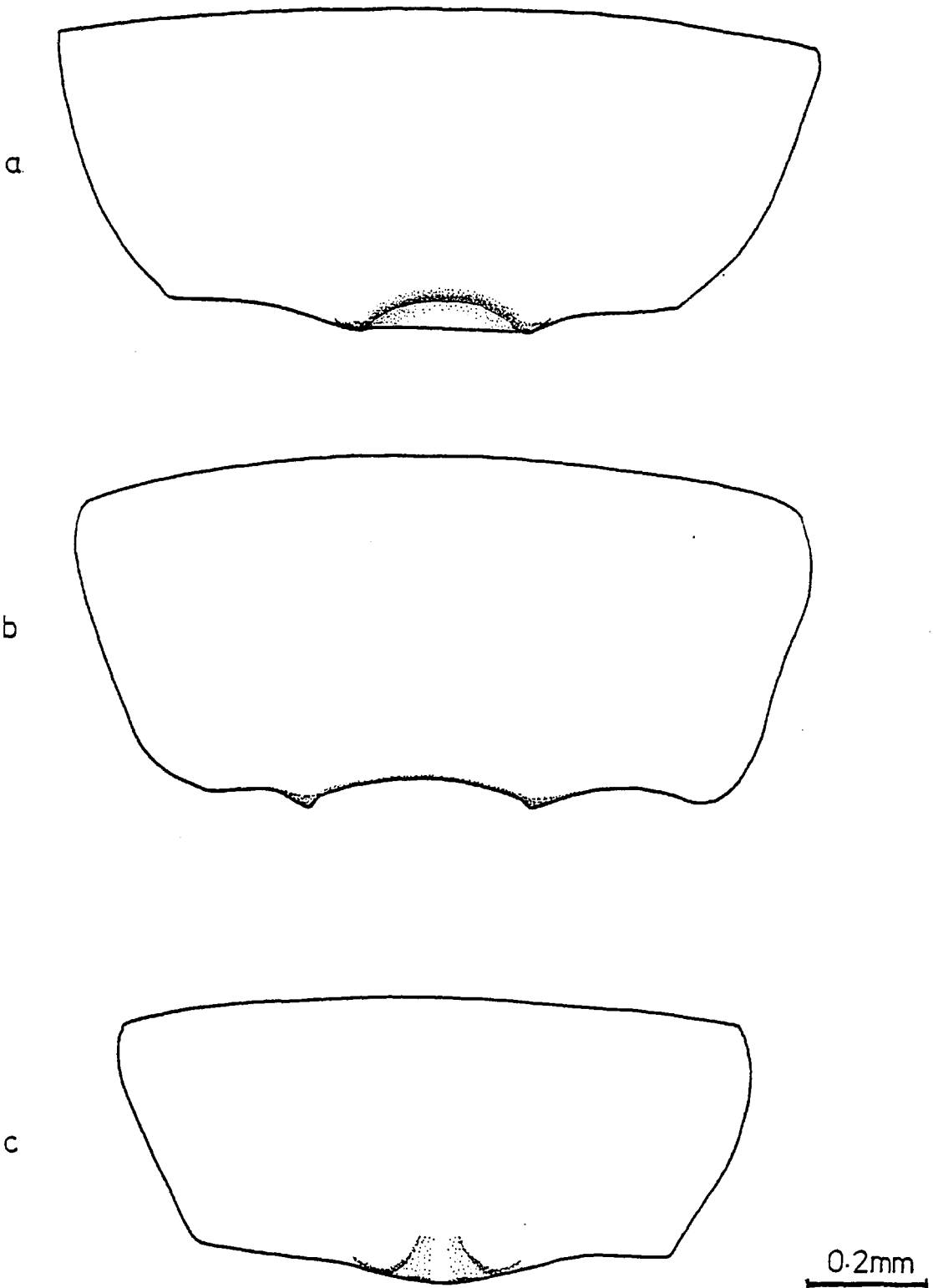


Fig.4.18 Male sternite VII of Platystethus, a) P.alutaceus, b) P.cornutus,
c) P.degener.



A. mutator (Lohse)

A. sculpturatus (Gravenhorst)

Distribution and Habitat

Detailed distribution is given by Horion (1963).

A. inustus

South-Palaeartic species: north Africa, Mediterranean area, north to extreme south Scandinavia. Common in western Europe but only sporadic in the east outside the Mediterranean area, Caucasus and Asia Minor.

A. mutator

Northwest Germany (Lohse, 1963)

Switzerland, Bulgaria, Romania, Yugoslavia, Bohemia (EMNH)

Britain, France, Czechoslovakia, restricted to higher altitudes in eastern Europe.

A. sculpturatus

Western Palaeartic species. North to north Scandinavia and Iceland. Range broadly overlapping with A. inustus.

In the British Isles A. sculpturatus is generally distributed and the most common of the three species. A. inustus is widely distributed but less common than A. sculpturatus except near the coast. A. mutator is known only from scattered localities in England and Scotland (Hammond, pers. comm).

All three species may be found together, most commonly in dung or carrion, but also in a wide range of other decaying organic matter.

Secondary Sexual Characters

These have been documented by Fagel (1956) and Hammond (1968).

The secondary sexual features in the group are not marked but these three species are exceptions.

A. inustus (Figs. 4.19b and 4.20b).

Sternite VII: two tubercles near the posterior margin with very sparse pubescence on their external side only. Anterior to the tubercles is a glabrous semi-circular area, not bordered by a fringe of setae.

Sternite VIII: the posterior border of characteristic shape.

Aedeagus: the apex of the median lobe with minor shape difference from A. sculpturatus and A. mutator.

: lateral lobes of characteristic shape.

A. mutator (Figs. 4.19c and 4.20c).

Sternite VII: two yellowish tubercles near the posterior margin bearing a sparse, dark pubescence on their posterior borders only. Anterior to the tubercles is a very shallow, ill defined impression which is glabrous and unpunctured and not bordered by a fringe of setae.

Sternite VIII: the posterior border of characteristic shape.

Aedeagus: the apex of the median lobe with minor difference in shape from A. inustus and A. sculpturatus.

: lateral lobes of characteristic shape.

A. sculpturatus (Figs. 4.19a and 4.20a).

Sternite VII: two yellowish tubercles near the posterior margin bearing a fringe of close yellow pubescence which extends over the tubercles and into the intervening space. Anterior to the tubercles is a deep impression with a well defined semi-circular anterior border bearing a fringe of setae. The impression is pubescent and closely punctured.

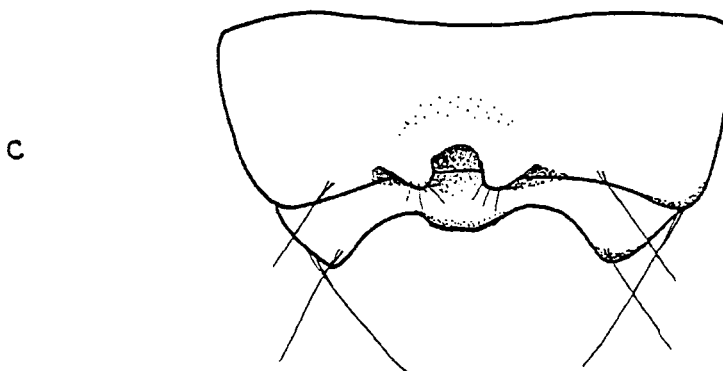
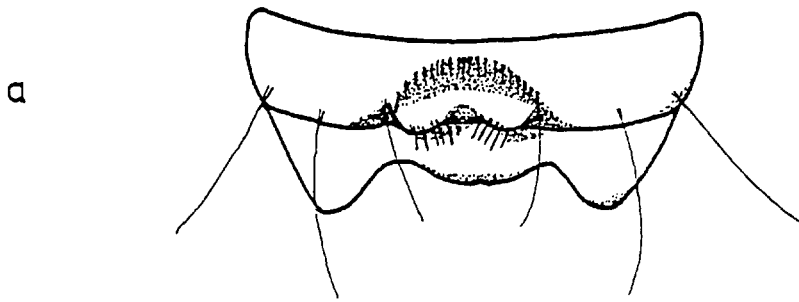
Sternite VIII: the posterior and border of characteristic shape.

Aedeagus: the apex of the median lobe with minor difference in shape from A. inustus and A. mutator.

: lateral lobes of characteristic shape.

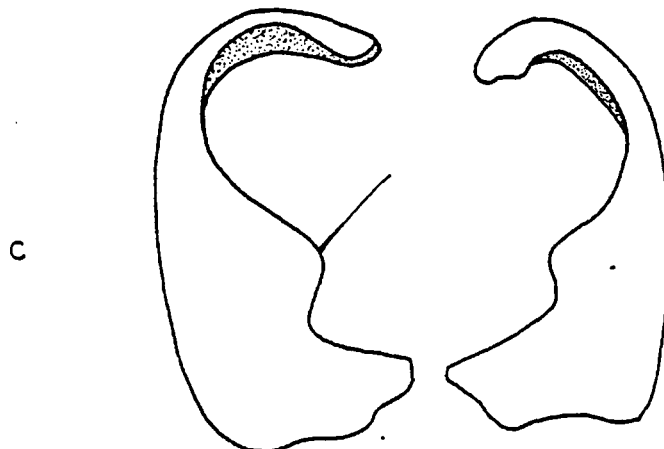
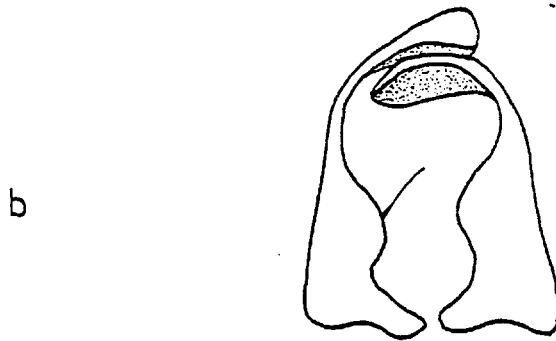
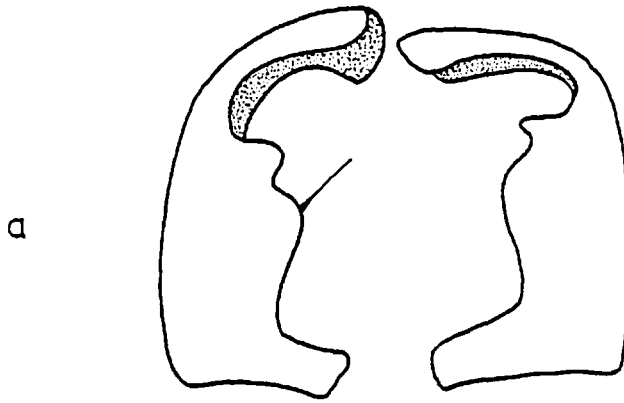
A. sculpturatus is the most widespread of the three species and has the most divergent secondary sexual characters. A. mutator seems

Fig.4.19 Male sternite VII and VIII of Anotylus, a) A.sculpturatus,
b) A.inustus, c) A.mutator.



0.5mm

Fig.4.20 Lateral lobes of the ♂ genitalia of Anotylus, a) A.sculpturatus,
b) A.inustus, c) A.mutator.



0.2mm

to be intermediate between A. sculpturatus and A. inustus.

A. inustus has the lateral lobes of the genitalia resembling those of other members of the species group.

A further species, A. hybridus Eppelsheim (unpublished), is reported from the Caucasus and northern Turkey (in high altitude areas; of patchy distribution). This species has very distinct external characters but shares identical secondary sexual features with A. mutator. It is found syntopically with A. inustus and A. sculpturatus and is likely to be a geographical replacement for A. mutator. However, there is considerable support for the view that A. mutator should be regarded as a subspecies of A. hybridus (Hammond, pers. comm.).

4.3.4. Paederinae.

Medon. Stephens

- M. apicalis (Kraatz)
M. brunneus (Erichson)
M. castaneus (Grav.)
M. dilutus (Erichson)
M. fuscus (Mannerheim)
M. nigritulus (Erichson)
M. pocoferus (Peyron)
M. ripicola (Kraatz)
M. rufiventris (Nordman)

Distribution and Habitat

Detailed distribution is given by Horion (1965).

M. apicalis

Western and southern Europe, sporadic in central and northern Europe, western north Africa, Madeira, Azores, north India.

M. brunneus

Central and southern Europe, north to Yorkshire in England, and southern Scandinavia.

M. castaneus

North and central Europe, southern England
Russia (BMNH).

M. dilutus

Central and southern Europe, isolated cases in northern Europe, Canary Islands, north Africa, Asia Minor.

M. dilutus is thought not to be British; existing British records are likely to be in error (Hammond, pers. comm.).

M. fuscus

Western and southern Europe, Caucasus, Asia Minor.

M. nigrutilus

Southern Europe. A subspecies in Mediterranean area and north Africa.

M. pocoferus

France, Italy, Algiers, Tunisia and England (BMNH).

M. ripicola

Western and southern Europe, central and southern north Europe, western north Africa, Azores, Madeira, north to Denmark and southern Sweden.

M. rufiventris

Southern and southern central Europe and western north Africa.

M. rufiventris, M. nigriventris and possibly M. dilutus do not occur in Britain.

The British distribution of these species is not well documented.

M. apicalis: Surrey, Sussex, Cambridgeshire (BMNH). South very seldom (Horion).

M. brunneus: Kent, Surrey, Devon, Sussex, Wales (BMNH).

M. castaneus: southern England.

M. fuscus: Surrey (BMNH)
England, seldom (Horion).

M. pocoferus: England, very rare (Joy, 1932).

M. ripicola: Herefordshire, south Devon, Dorset (BMNH).
England, seldom (Horion).

The species are found syntopically, and some may be closely related, but little is known of their relationships.

Most of the species occur in rotting plant matter stack debris,

litter, moss and underground nests.

Secondary Sexual Characters

The seventh and sometimes eighth sternites in the male have their posterior margins modified in shape and fringed with filiform and peg-setae in a characteristic pattern for each species (Fig. 4.21).

The apex of the median lobe in all species is very strikingly modified and distinctly different (Fig. 4.21).

Lithocharis

L. distinguendus Cameron

L. fuscipennis Kraatz

L. lamellifer Cameron

L. nigriceps Kraatz

L. ochracea (Gravenhorst)

L. penicillata Cameron

L. sordidus Cameron

L. somrcula Kraatz

L. vilis Kraatz

These species are likely to be of Asian origin, only L. nigriceps and L. ochracea occurring in Britain. All are very closely allied and of very similar appearance.

Distribution and Habitat

L. distinguendus Singapore, Malaya, north Borneo (Cameron, 1931).

L. fuscipennis

Malaya, Ceylon, Sumatra (Cameron, 1931)
and south-east Asia.

L. lamellifer

India (Cameron, 1931).

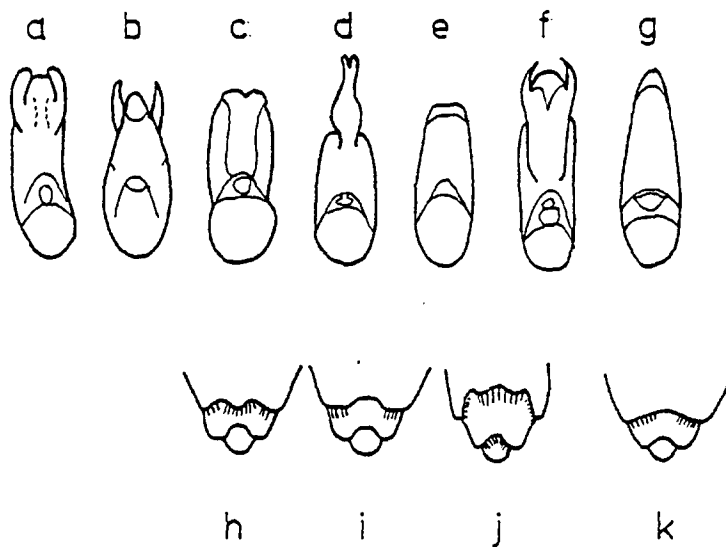
L. nigriceps

Almost cosmopolitan. Ceylon and widely
distributed in the Asiatic region (India,

Fig.4.21 Male genitalia and apical abdominal sternites of Medon

(after Freude, Harde & Lohse, 1964),

a-g ♂ genitalia, a) M.rufiventris, b) M.nigritulus, c) M.apicalis,
d) M.ripicola, e) M.fuscus, f) M.dilutus, g) M.brunneus;
h-k ♂ abdominal sternites, h) M.apicalis, i) M.ripicola,
j) M.fuscus, k) M.brunneus.



China and Japan). Europe, north to Scandinavia (Horion), New Zealand, North America.

L. ochracea

Almost cosmopolitan in temperate and warm zones. Generally distributed in south and central Europe, north to southern Scandinavia (Horion).

L. penicillata

India (Cameron, 1931). Malay Peninsula, Singapore, south China.

L. sordidus

Malay Peninsula.

L. sororcula

Ceylon, Singapore, West Indies, south-east Asia (Cameron, 1931).

L. vilis

Ceylon, Penang, Singapore, Samoa (Cameron, 1931).

Also in the Neotropical region.

L. nigriceps and L. ochracea are both widely distributed in the British Isles, and are found in a similar range of habitats, sometimes syntopically.

The range of habitats for L. nigriceps and L. ochracea are similar, the species occurring in rotting vegetable matter, moss, dung, hay and synanthropic habitats such as compost, where there is some evidence that L. nigriceps is displacing L. ochracea in many parts of Europe (Hammond, pers. comm.).

L. fuscipennis is recorded from carrion and rotting fruit, L. vilis from rotting fruit, and L. penicillata and L. sororcula from dung. Other species of the genus have been taken in a wide range of synanthropic habitats, while some are dung specialists (Blackwelder, 1943).

Secondary Sexual Characters

The females of all the species are extremely difficult to separate; the males are readily distinguishable by the very strongly marked abdominal secondary sexual characters.

Sternite VII: (Figs. 4.22a, 4.23a, 4.24a&c, 4.25a,c & e, 4.26a & c).

The posterior margin is emarginate bearing a fringe of elongate, black peg setae. The precise shape of the emargination and the extent, length and pattern of the peg setae is distinct in each species.

Groups of longer black setae are also present at the lateral edge of the peg setal fringe in L. ochracea and L. nigriceps, and single yellow setae overlie the peg seta fringe in L. fuscipennis, L. lamellifer, L. penicillata. L. somnula is unique in having long, stout, black setae overlying the peg seta fringe.

Sternite VIII: (Figs. 4.22b, 4.23b, 4.24b & d, 4.25b, d & f, 4.26b & d).

The posterior margin is deeply and triangularly emarginate with individual shape differences in the different species. L. lamellifer has a central quadrate lobe projecting from the emargination. Long setae, individually or grouped, are in characteristic sites in the individual species.

Aedeagus: the two closely related and syntopic British species (L. nigriceps and L. ochracea) exhibit very striking differences in the aedeagus (Fig. 4.22c and 4.23c).

Note: the only record of mating behaviour in the Paederinae is of Rugilus orbiculatus (Payk.) (Section 5.2.10) which does not have secondary sexual features of the type described for Medon and Lithocharis.

Fig.4.22 Lithocharis ochracea, a) ♂ sternite VII, b) ♂ sternite VIII
c) aedeagus.

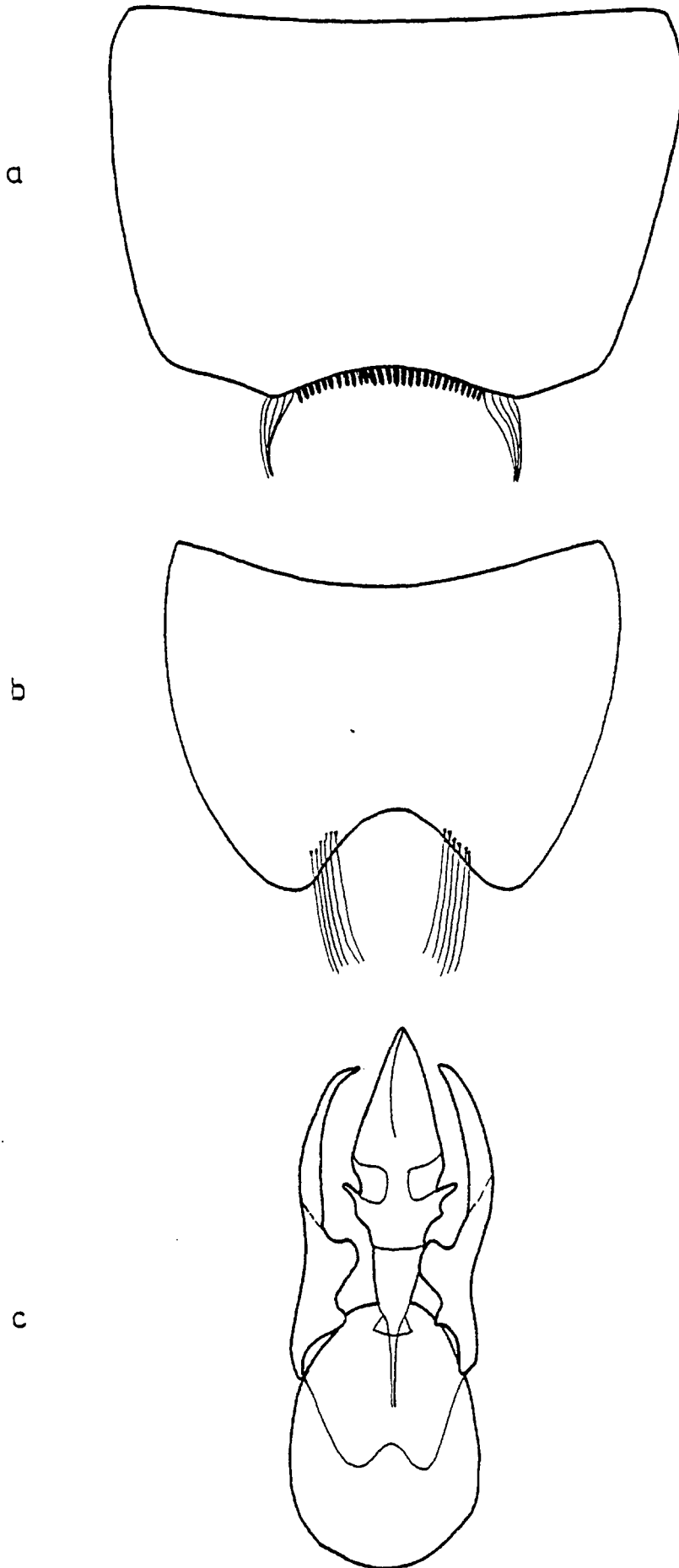


Fig.4.23 Lithocharis nigriceps, a) ♂ sternite VII, b) ♂ sternite VIII, c) aedeagus.

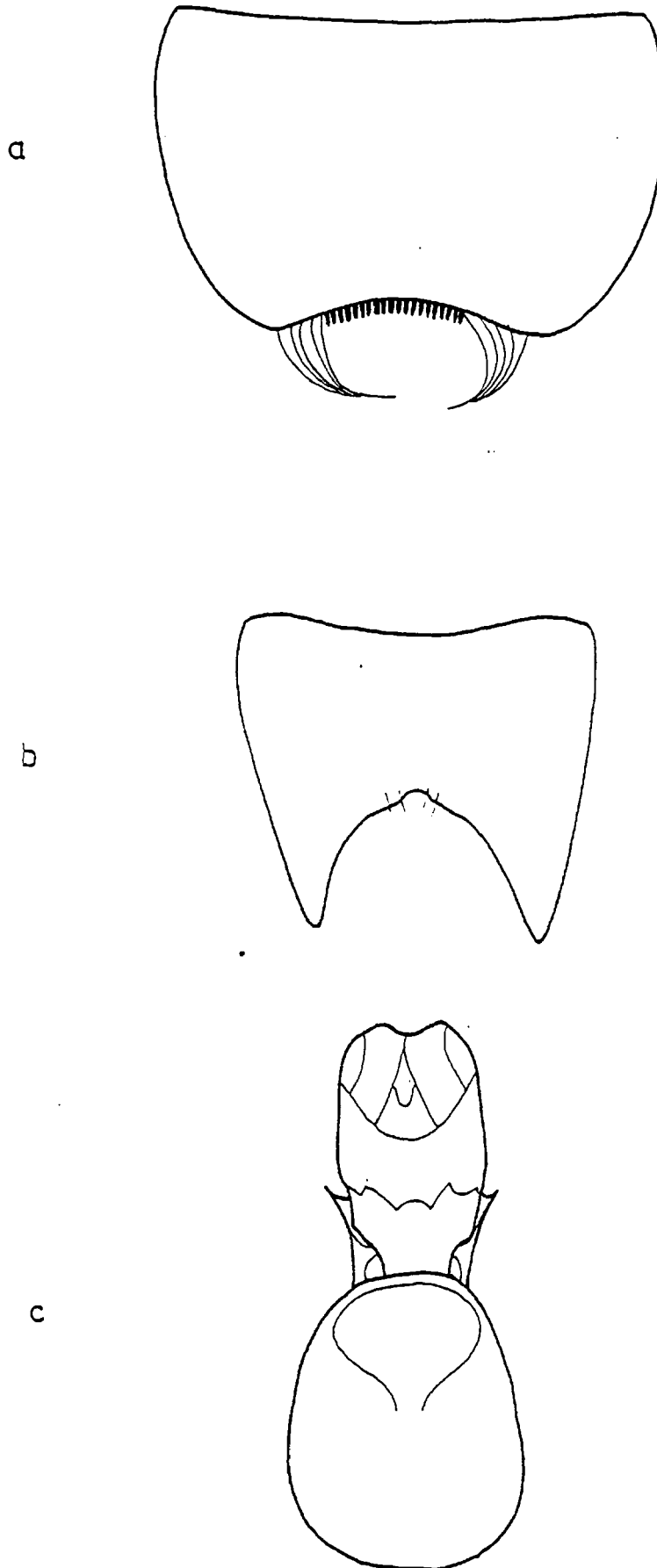
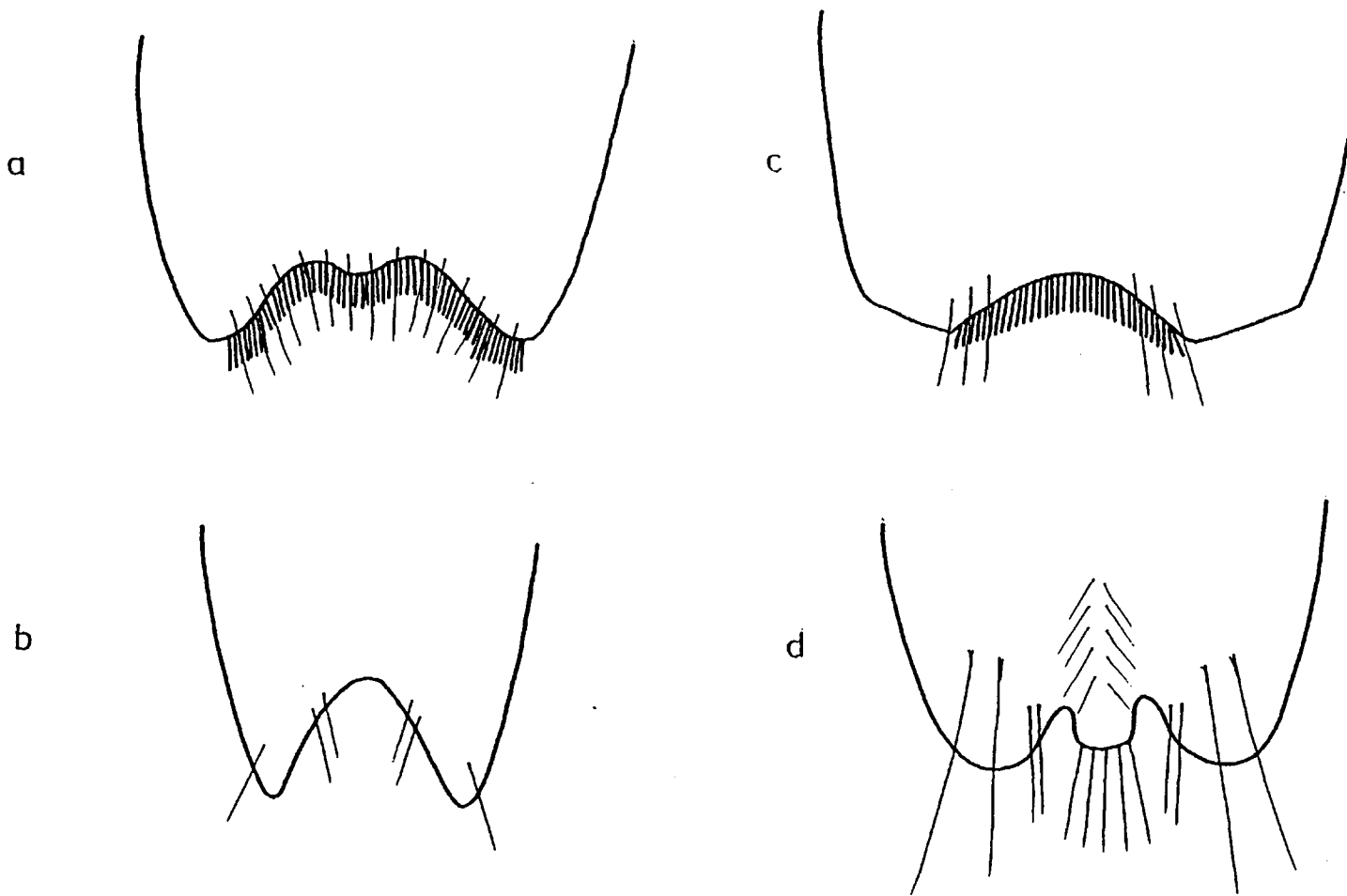


Fig.4.24 Lithocharis fuscipennis, a) ♂ sternite VII, b) ♂ sternite VIII, L.lamellifer, c) ♂ sternite VII, d) ♂ sternite VIII.



0.2mm

Fig.4.25 Lithocharis sororcula, a) ♂ sternite VII, b) ♂ sternite VIII, L. penicillatus, c) ♂ sternite VII, d) ♂ sternite VIII, L. vilis, e) ♂ sternite VII, f) ♂ sternite VIII.

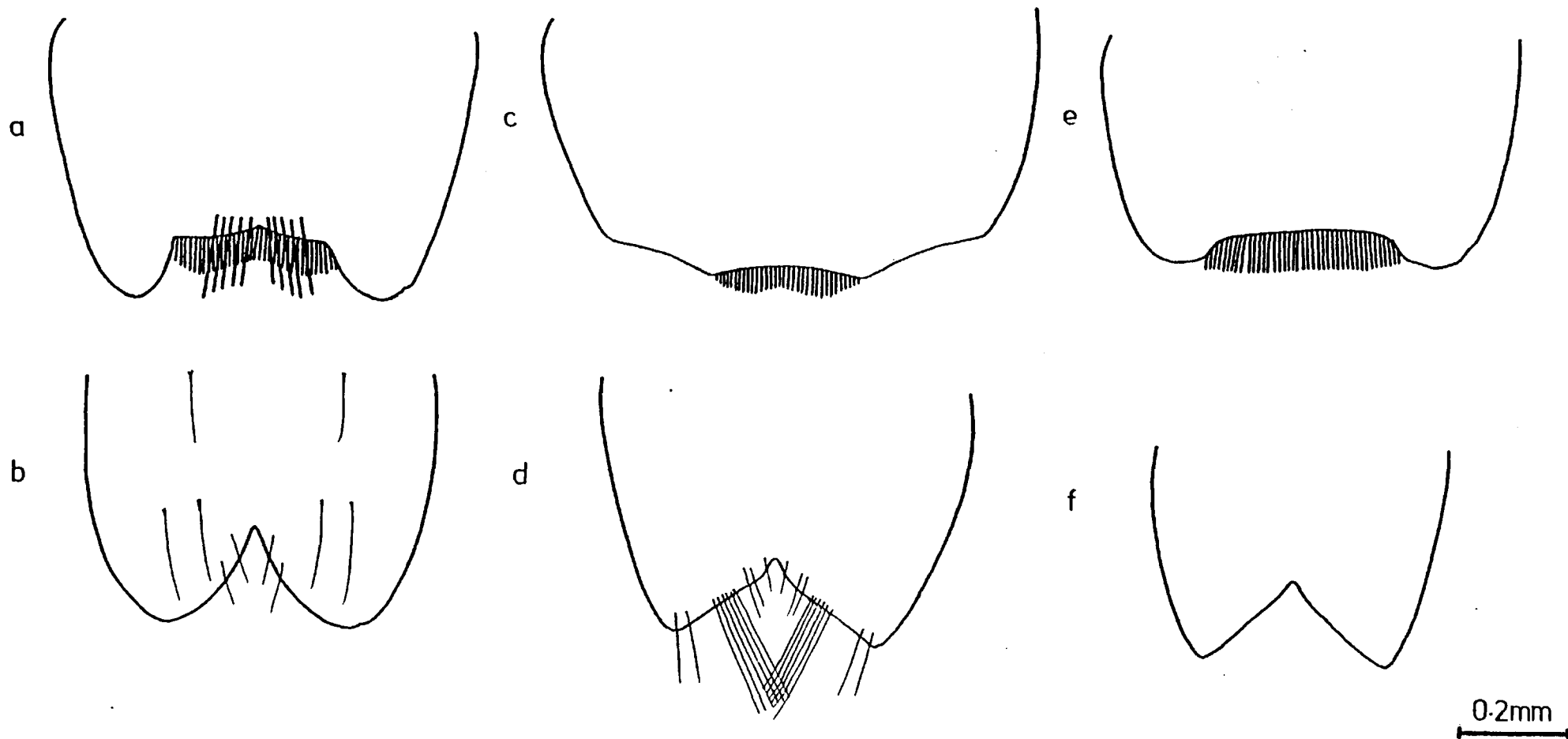
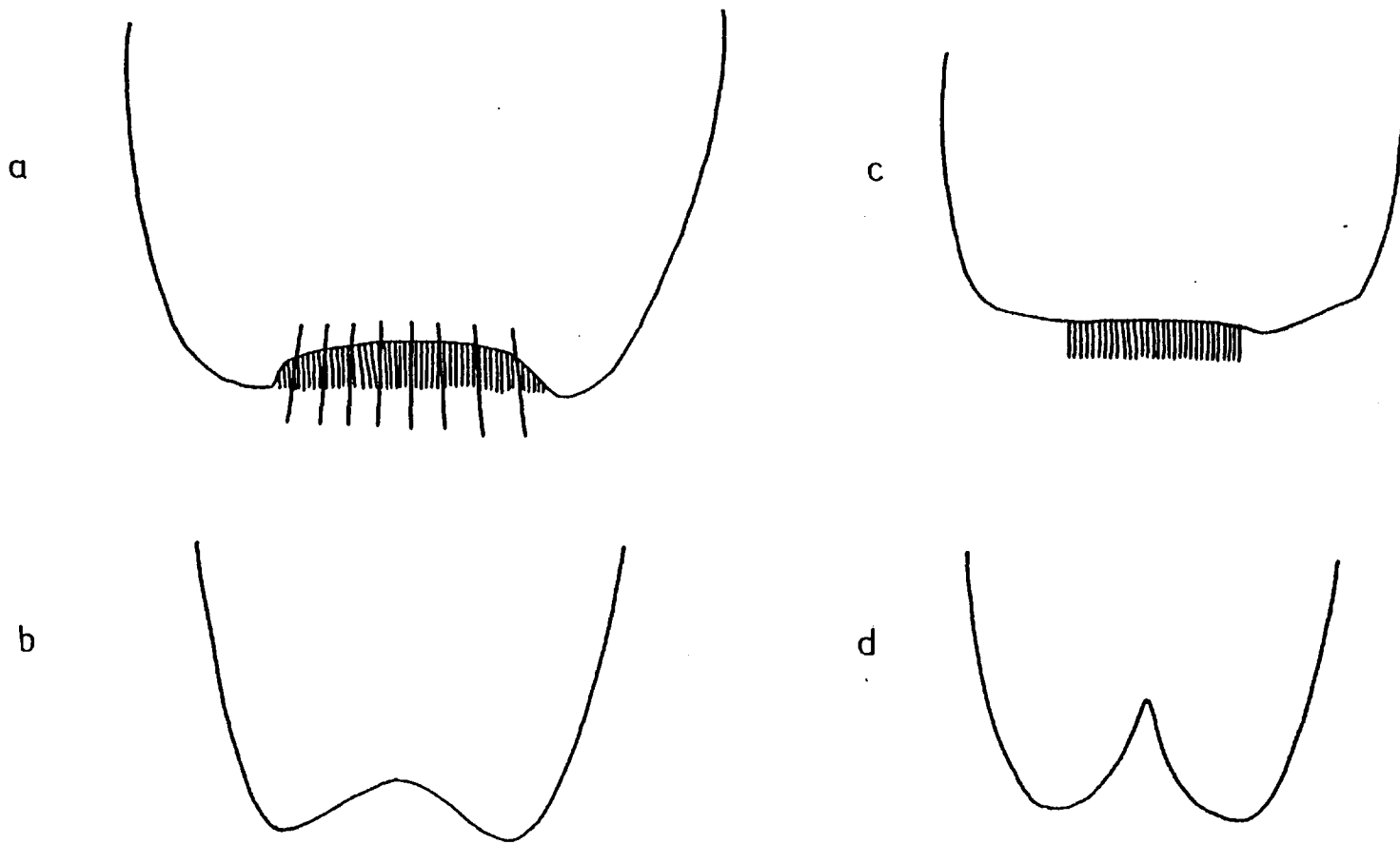


Fig.4.26 Lithocharis distinguendus, a) ♂ sternite VII, b) ♂ sternite VIII, L.sordidus, c) ♂ sternite VII, d) ♂ sternite VIII.



0.2mm

4.3.5 Staphylininae

The subfamily Staphylininae is very large and diverse comprising five tribes according to Newton (pers. comm. Section 7).

Distribution of male secondary sexual characters in the tribe

Staphylinini

- Thoracic: i) expansion of the fore-tarsus is of frequent occurrence.
- ii) other leg modification, e.g. spines.
- Abdominal: i) modification of the seventh sternite.
- ii) emargination of the posterior margin of the eighth sternite is of frequent occurrence.
- Genitalic: i) the median lobe apex is often of characteristic form in a species and its modification may be elaborate.
- ii) the form of the lateral lobe is frequently characteristic of a species and, like the median lobe, its modification may be elaborate.
- iii) the number and siting of peg setae on the lateral lobe is frequently characteristic of a species.

Tables 4.1a - d give the distribution of the most striking types of secondary sexual characters in the five tribes of the Staphylinini, those of common occurrence are not included. The tables include only those genera where specimens, or figured descriptions are available.

Philonthina

Philonthus Stephens

i) Variation in secondary sexual characters

The male secondary sexual characters in Philonthus consist of:

1. An emarginate eighth sternite, the depth of which is somewhat variable. Although it differs between species, it is unlikely to be used as a tactile recognition feature and is more probably concerned

TABLE 4.1a

Secondary Sexual Characters in the Xanthopygina

Genus	leg modification			abdominal modification			elaborate	elaborate	peg setae
	fore	mid	hind	7	8	9	median lobe	lateral lobe	
Agacerus	-				-		-	-	-
Agelosus	-				-		-	-	+
Allosthenopsis	-				-		-	-	
Amelinus	-				-		-	-	+
Brachydirus	-			♂ ST	♂ ST		-	+ curved	+
Eugastus	-				-		+ t	-	+
Gastrisus	-				-		+ t	-	+
Glenus	-				-		-	-	+
Hadropinus	-				-		+	-	-
Hadrotes	-			♂ ST			-	-	-
Lampropygyus	-				-		-	-	
Liusus	-				-		-	-	-
Ocyolinus	-				-		-	-	
Pannegus	-				-		-	-	+ t
Paraxenopygyus	-				-		-	-	
Phanolinus	-				-		+ t	-	+
Philothalpus	-				-		+ t	-	+
Plociopterus	-			♂ ST, ♀ T, ♂ ST	♂ ST		-	-	+
Quediosoma	-				-		-	-	+
Styngetus	-	orempilate fem.			-		+ t	-	+
Thinopinus	-				-		+	-	-
Trigonopselaphus	-				-		+ t	-	+
Tympanophorus	-			♂ ST			-	-	+
Xanthopygyus	-			♂ ST			+ t	-	+
Xenopygyus	-				-		+ t	-	+

t = tooth-like pegs.

TABLE 4.1b

Secondary Sexual Characters in the Staphylinina

Genus	leg modification			abdominal modification			elaborate median lobe	elaborate lateral lobe	peg setae
	fore	mid	hind	7	8	9			
Abemus	-			♂ ST			-	-	-
Alapsodus	-				-		-	-	- sp.
Atlantogoerus	-				-		-	-	-
Barygnathus	-				-		-	-	?
Craspedomerus	-				-		-	-	-
Creophilus	-				-		-	-	- sp.
Dinothenarus	-				-		+	-	+
Emus		♂ h.troch		♂ ST			-	-	-
Erichsonellus	-				-		+	-	-
Eucibdelus	-				-		-	-	-
Goerius	-				-		-	-	?
Leistotrophus	-			♂ ST			-	-	-
Menoedius	-			♂ ST			-	-	-
Metocypus	-				-		-	-	-
Nadolia	-			♂ ST			-	-	-
Ocypus	-				-		+ -	-	-
Ontholestes	-				-		-	-	-
Palaestrinus	-				-		-	-	+ (sm)
Parabemus	-				-		+	-	+
Parapalaestrinus	-			♂ ST			-	-	?
Physetops	-				-		-	-	-
Platydracus	-				-		+	-	-
Protogoerus	-				-		-	-	-
Pseudocypus	-				-		-	-	-

TABLE 4.1b (contd.) Secondary Sexual Characters in the Staphylinina

Genus	leg modification			abdominal modification			elaborate	elaborate	peg setae
	fore	mid	hind	7	8	9	median lobe	lateral lobe	
Rhynchocheilus	-				♂ T		-	-	+
Seleucus	-				-		-	-	+
Staphylinus	-				-		+	-	+ sp
Tasgius	-				-		-	-	-
Thoracostromylus	-			♂ ST			+	-	-
Trichocosmetes	-				-		-	-	+

sp. = spicules/pegs

sm. = small

TABLE 4.1c

Secondary Sexual Characters in the Philonthina

Genus	leg modification			abdominal modification			elaborate	elaborate	peg setae
	fore	mid	hind	7	8	9	median lobe	lateral lobe	
Actinus		-			-		+	-	-
Afrorabigus		-			-		-	-	+
Amichrotus		-			-		-	-	+
Belonuchus	♂ fem	-	♂ fem		-		+	-	+
Cafius		-			-		+	-	+
Chroaptomus		-			-		-	-	-
Diatrechus		-			-		+	-	+
Endeius		-			-		+	-	-
Erichsonius		-			-		-	+	+
Gabrius	♂ fem	-	♂ fem		-		-	-	+
Gabronthus		-			-		-	-	+
Hesperopalpus		-			-		-	-	
Hesperus		-			-		-	-	+
Jureceкия		-			-		-	-	+
Leptopeltus		-			-		-	-	-
Leucitus		-			-		-	-	-
Linoderus		-			♂ ST		-	-	-
Misantlius		-			-		-	-	+
Musicoderus	♂ fem	-	♂ fem		-		-	-	-
Mysolius		-			-		-	-	-
Neobisnius		-			-		-	-	+
Odontolinus	♂ fem	-	-		-		-	-	-
Onthostygnus		-			-		-	-	-

TABLE 4.1c (contd.) Secondary Sexual Characters in the Philonthina

Genus	leg modification			abdominal modification			elaborate	elaborate	peg setae
	fore	mid	hind	7	8	9	median lobe	lateral lobe	
Orthidus		-			-		+	-	+
Paederomimus	♂ fem				-		-	-	-
Palaeophilonthus		-			-		+	-	+
Paragabrius		-			-		-	-	+
Philonthus		-			-		-	+	+ -
Phucobius		-		♂ ST			+	-	+
Rabigus		-			-		-	-	+
Remus		-			-		+	-	+
Spatulonthus		-			-		-	-	+
Stevensia		-			-		-	-	+
Thinoxaius		-			-		+	-	+
Tolmerinus		-			-		-	-	+

TABLE 4.1d

Secondary Sexual Characters in the Quedina and Amblyopinina

Genus	leg modification			abdominal modification			elaborate	elaborate	peg setae
	fore	mid	hind	7	8	9	median lobe	lateral lobe	
<u>QUEDIINA</u>									
Acylophorus	-				-		-	-	+
Algon	-				-		-	-	+
Anaquedius	-				-		-	-	+
Anchocerus	-				-		-	-	-
Astrapaeus	-				-		-	-	-
Atanygnathus	♂ f.	fem.	brush		-		-	-	-
Cafioquedius	-				-		+	-	-
Cheilocolpus	-				-		-	+	-
Cordylaspis	-				-		-	-	-
Cyrtothorax	-				-		-	-	+
Euryporus	-				-		+	-	+
Haemotodes	-			♂ ST			+	-	+
Hasumius	-				-		+	-	+ t
Heinzia	-				-		+	-	+
Hemiquedius	-				-		-	-	+
Heterothops	-				-		-	-	-
Loncovilius	-				-		-	+	+ t
Moerxerus	-				-		+	-	-
Myotyphlus	-				-		-	+	-
Pseudorientis	-				-		-	-	+
Quedimacrus	-				-		-	-	+
Quedionuchus	-				-		+	-	+
Quediopsis	-				-		-	-	+ t
Quedius	-				-		+	-	+

TABLE 4.1d (continued) Secondary Sexual Characters in the Quedina and Amblyopinina

Genus	leg modification			abdominal modification			elaborate	elaborate	peg setae
	fore	mid	hind	7	8	9	median lobe	lateral lobe	
Sphingoquedius	-			-			-	-	+ t
Triacrus	-			-			-	-	+
Termitoquedius	-			-			-	-	
Velleius	-			-			+	-	+
<u>AMBLYOPININA</u>									
Amblyopinodes	-			-			-	+	+ t
Amblyopinus	-			-			-	-	+ t
Edrabijs	-			-			-	+	+ t

with extrusion and positioning of the aedeagus during mating.

2. The fore tarsus may be expanded in males of some species.

3. The most distinct characters are of the aedeagus, particularly the apex of the median lobe, the form of the lateral lobe, and the pattern of peg setae on the inner surface of the lateral lobe.

The pattern is often very different in closely related sympatric species.

The range of variation within a single genus is marked, some of the most elaborate extremes being found in African and Asian species. Figures 4.27 and 4.28 illustrate the extremes of variation in peg patterns. Tables 4.2a&b list the different character states of the genitalia found within the genus. This is based on deviations from the most abundant type of genitalia which is similar to P. sordidus.

ii) Comparisons of species groups

An examination of African and European species groups is presented to further illustrate the range of variation within the genus, and to compare species which are thought to be closely allied (Tottenham, 1949, 1955 & 1962).

Philonthus reinecki-Group

This is a closely related group of African Philonthus which occur in elephant, cow and white rhinocerus dung.

Philonthus species are grouped by many authors according to the number of punctures in the pronotal discal series (Coiffait, 1974). This is clearly an artificial method of grouping although in many cases (e.g. P. sordidus-group) this may coincide with close relationship.

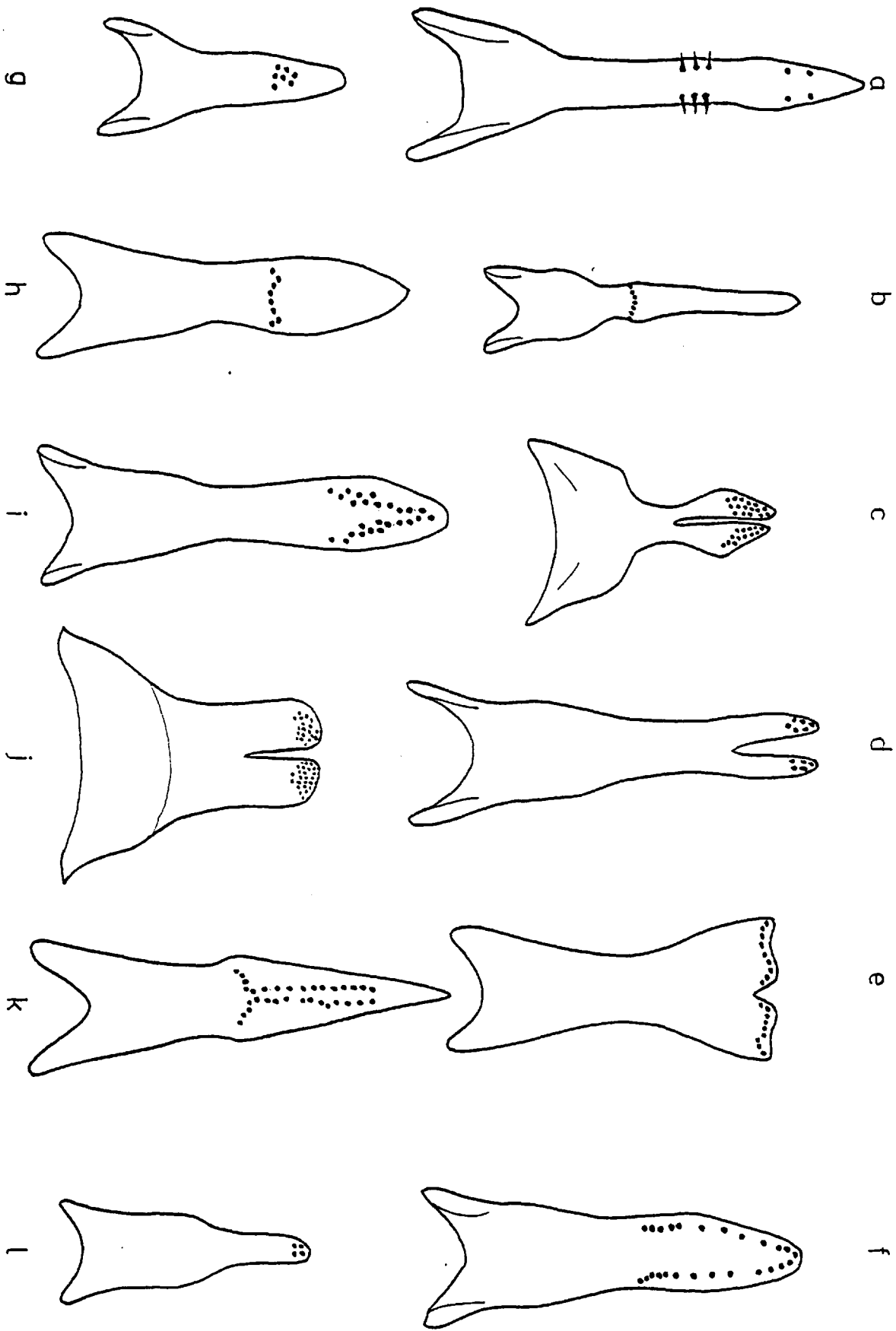
In the P. reinecki group the number of punctures in the discal series varies from 0, 1, 2, to 3.

P. curiosus Tottenham

P. reinecki Schubert

Fig.4.27 Lateral lobes of male genitalia in species of Philonthus, to show patterns of peg setae,

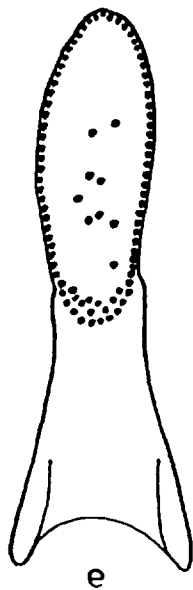
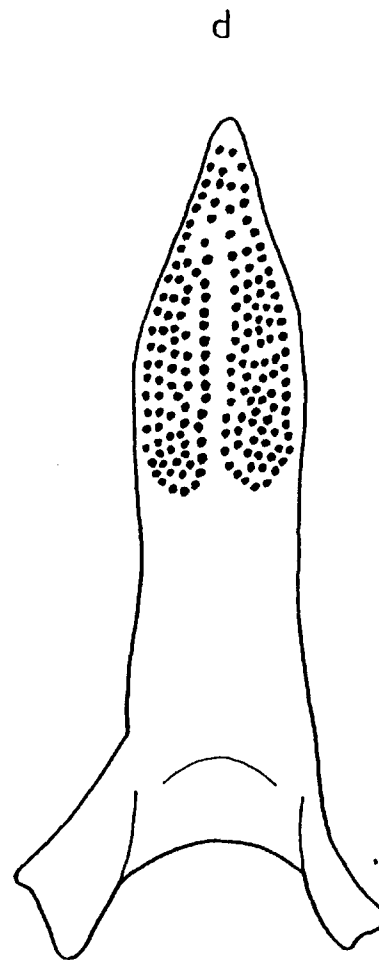
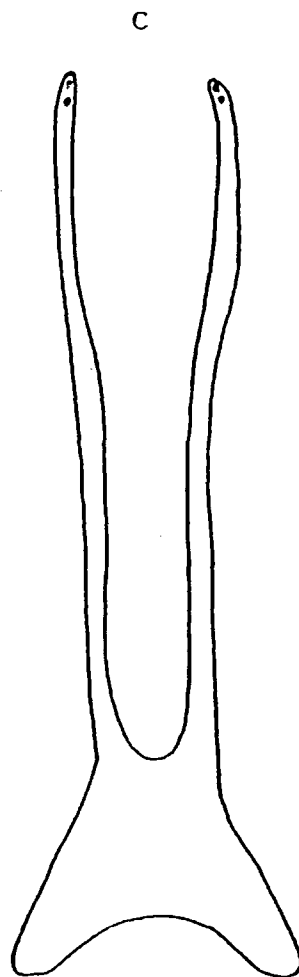
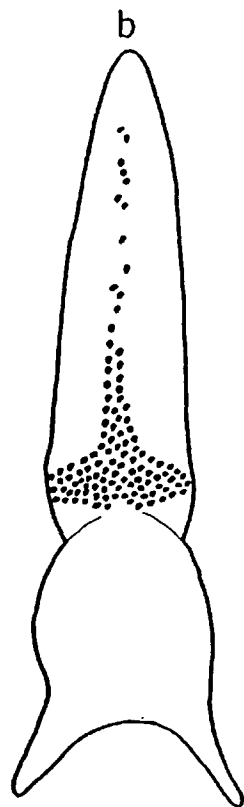
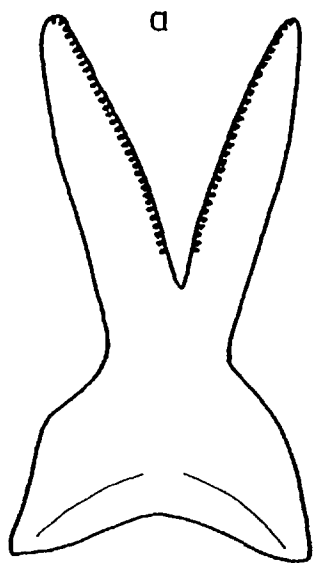
- a) P.pellax, b) P.paederomimus, c) P.biguttulus, d) P.morio,
- e) P.fimetarius, f) P.sordidus, g) P.constricticeps,
- h) P.sparsus, i) P.cephalotes, j) P.bulbifer, k) P.varius,
- l) P.variipennis,



0.2mm

Fig.4.28 Lateral lobes of male genitalia in species of Philonthus, to show patterns of peg setae,

- a) P.turbidus, b) P.lucanicornis, c) P.pollux, d) P.proximus,
e) P.jurgans.



0.2mm

TABLE 4.2a States of genitalia in African *Philonthus* species (Deviations from a common form e.g. *P. sordidus*)

<u>Median Lobe</u>	1. Shape	- globular e.g. <i>P. tumulinus</i> Tott.	
		- elongate	
	2. Hooked processes at apex	e.g. <i>P. rapaciosus</i> Tott., <i>P. clambus</i> Tott.	
	3. Extreme curvature at apex	e.g. <i>P. turbidus</i> Er.	
	4. Asymmetry	e.g. <i>P. monticola</i> Bernh.	
<u>Lateral Lobe</u>	1. Entire		
	2. Bilobed	- lobes close or distant e.g. <i>P. reinecki</i> Schub. <i>P. curiosus</i> Tott.	
		- extreme or not extreme bilobing e.g. <i>P. pollux</i> Fauv.	
		- individual lobes bilobed e.g. <i>P. schoutedini</i> Bernh.	
	3. 4-Lobed	- e.g. <i>P. schoutedini</i> Bernh.	
	4. Size	- small compared with median lobe e.g. <i>P. aurantiacus</i> Tott.	
		- exceeding length of median lobe e.g. <i>P. irritans</i> Tott.	
	5. Asymmetry	- lobes of unequal length e.g. <i>P. bicoloripennis</i> Bernh. <i>P. sanguineus</i> Fauv.	
	6. Pegs	- rounded	
		- tooth-like e.g. <i>P. pellax</i> Tott.	
		- all variations in arrangement e.g. <i>P. rulipennis</i> Fauv.	
	7. No Pegs		
	8. Central Division		

TABLE 4.2b States of genitalia in American Philonthus species (Deviations from a common form e.g. P. sordidus)

<u>Median Lobe</u>	1. Hooked at apex	e.g. <u>P. alutaceus</u> Horn
<u>Lateral Lobe</u>	1. Bilobed	e.g. <u>P. siegwaldi</u> Horn
	2. Asymmetry	e.g. <u>P. aurulentus</u> Horn
	3. Short compared to median lobe	e.g. <u>P. semiruber</u> Horn
	4. Reduced number of pegs	e.g. <u>P. puberulus</u> Horn
	5. Central Division	e.g. <u>P. puberulus</u> Horn

New Guinea Philonthus species

<u>Median Lobe</u>	Hooked at apex	e.g. <u>P. assecta</u> Last, <u>P. cheesmani</u> Cam
<u>Lateral Lobe</u>	Reduction in size	e.g. <u>P. apicornis</u> Guér.

Asiatic Philonthus species

<u>Lateral Lobe</u>	1. Bilobed/Entire	e.g. <u>P. lewisius</u> Sharp
	2. Pegs - increased number	e.g. <u>P. proximus</u> Kr.
	- decreased number	e.g. <u>P. variipennis</u> Kr.
	3. Central Division	e.g. <u>P. diallus</u> Tott.

Distribution and HabitatP. curiosus

Northwest Rhodesia, Kashitu; South Africa 7 miles west of Potgietersrus in cow dung; Emali Range, Sultan Hamud at 4900-5900¹.

P. reinecki

Rhodesia, Salisbury; Wankie Game Reserve, Rhodesia in elephant dung; South Africa, Mkuze Game Reserve, Natal in white rhinoceros dung; South Africa, near Ondangua in elephant dung.

The number of punctures in the discal series has been found to vary between 0 and 1 in both species.

P. reinecki was thought to be synonymous with P. curiosus, since they are almost indistinguishable in external morphology. The median lobes are very similar. However, the patterns of the somewhat elongate peg setae on the lateral lobe are distinct; P. reinecki has a clear margin around the pegs, although in P. curiosus the pegs extend to the apical margin of the lateral lobe. (Fig. 4.29).

Also in the same group are:

P. cinctipennis Fauvel (Fig.4.30)

P. ochrigonalis Tottenham (Fig.4.30)

Distribution and HabitatP. cinctipennis

Kenya, in elephant dung.

P. ochrigonalis

South Sudan, Yirol in elephant dung.

P. schoutedini Bernh., from Haut-Vele, is somewhat unique having almost smooth elytra, and an extraordinary development of the lateral lobe. Specimens of P. schoutedini have not been seen and Tottenham gives no indication of the numbers of specimens on which the description is based. This species belongs to a group closely allied to

Fig.4.29 Male genitalia of Philonthus; i. median lobe, ii. median lobe apex, iii. lateral lobe, a) P.reinecki, b) P.curiosus.

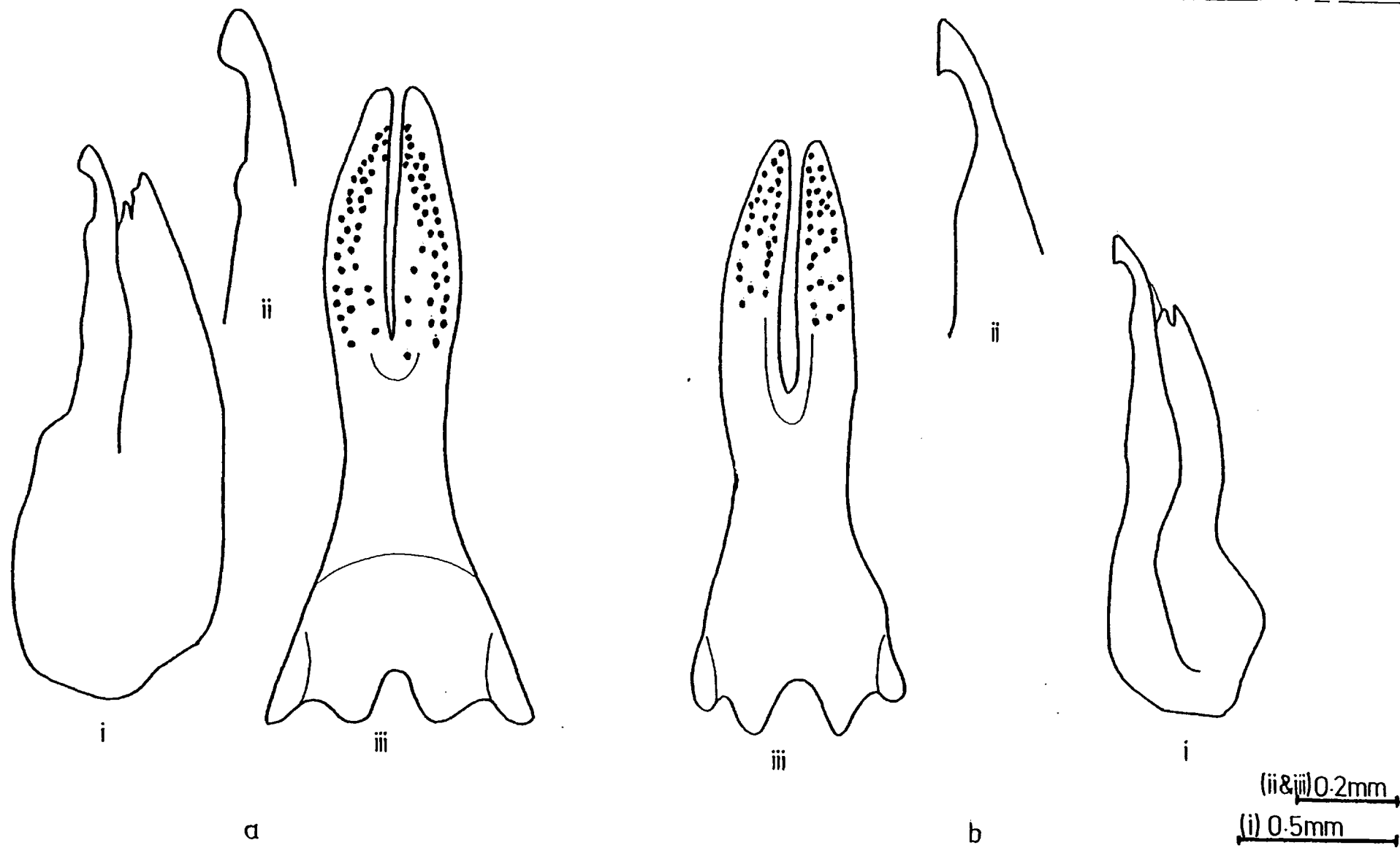
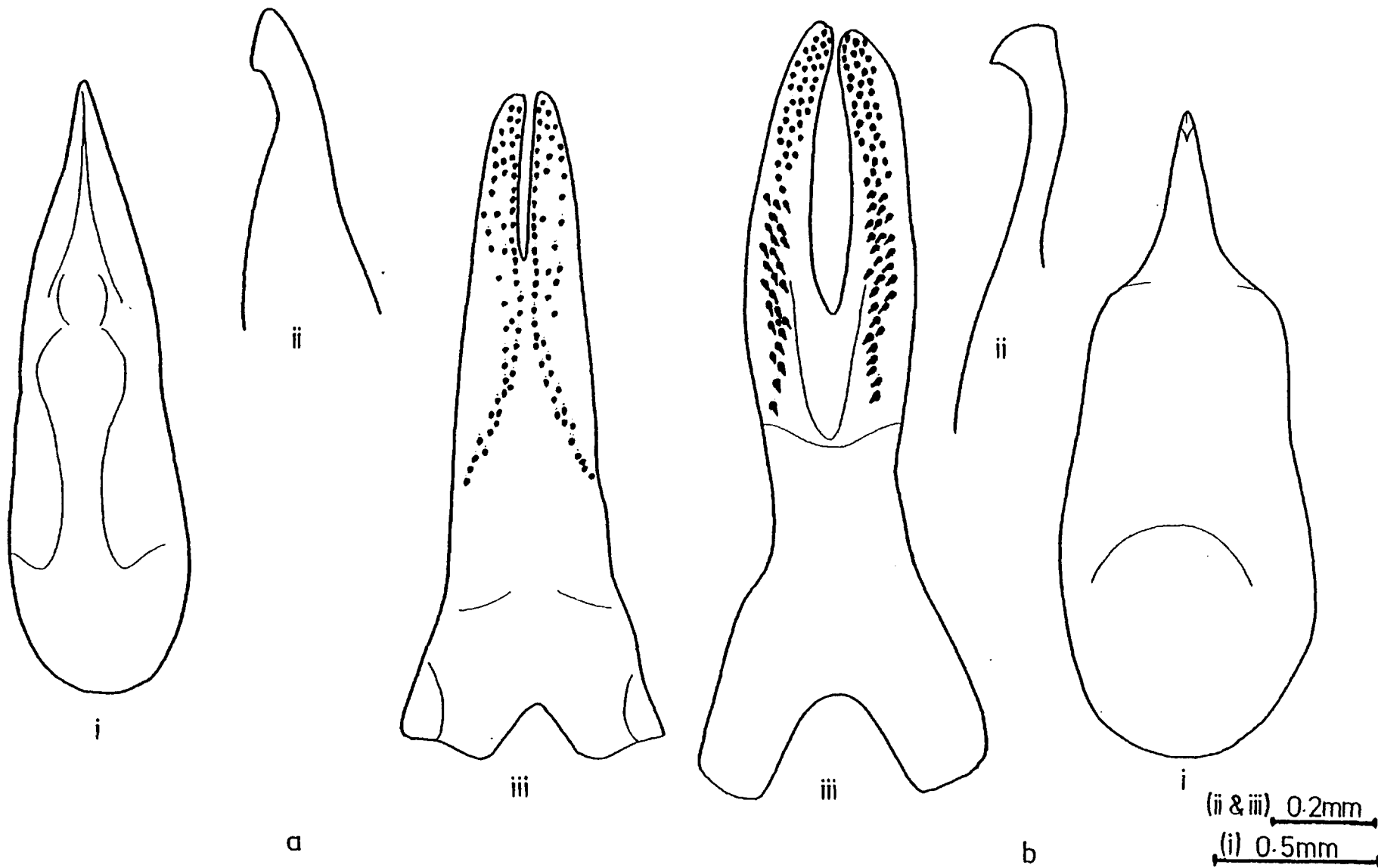


Fig.4.30 Male genitalia of Philonthus; i.median lobe, ii.median lobe apex, iii. lateral lobe, a) P.ochrigonalis,
b) P.cinctipennis.



P. reinecki but grouped together because their most distinguishing character is a series of large punctures on each elytron.

The group (Figs. 4.31-4.35) includes:

- P. descarpentriesi Levasseur (Congo)
- *P. dilucidus Tottenham (Nigeria, Entebbe)
- P. dilutior Bernhauer (Congo)
- P. lampropterus Bernhauer (Kivu, Kikumba)
- P. mongendensis Bernhauer (Congo)
- P. odzalensis Levasseur (Congo)
- P. schoutedini Bernhauer (Haut-Vele; Dika)
- *P. triseriatus Bernhauer (Congo)
- *P. tristichus Cameron (central Africa)
- *P. sp. 1. undescribed (South Africa, Natal,
Kenya, southwest Africa)

Another group of species, members of which may be closely allied, exhibit minor differences in external morphology and have different genitalia (Figs. 4.36-4.38).

- P. capeneri Last (Angola)
- P. cinctus Fauvel (sympatric with P. marginipennis)
- P. marginipennis Wollaston (southwest Africa, Angola
South Africa, Botswana)
- P. mivutanus Tottenham (south and southwest Africa
Rhodesia, Kenya)
- P. nairobiensis Cameron (east and southwest Africa,
Angola)
- P. parvicornis Fauvel (sympatric with P. cinctus
and P. marginipennis)
- P. stercorosus Tottenham (south Rhodesia)
- P. sp. 2. undescribed (southwest Africa, Rhodesia)

* species housed in BMNH.

Fig.4.31 Male genitalia of Philonthus; i. median lobe, ii. median lobe apex, iii. lateral lobe, a) P.descarpentriesi, b) P.odzalensis, c) P.dilutior, d) P.schoutedini. (after Tottenham, 1962).

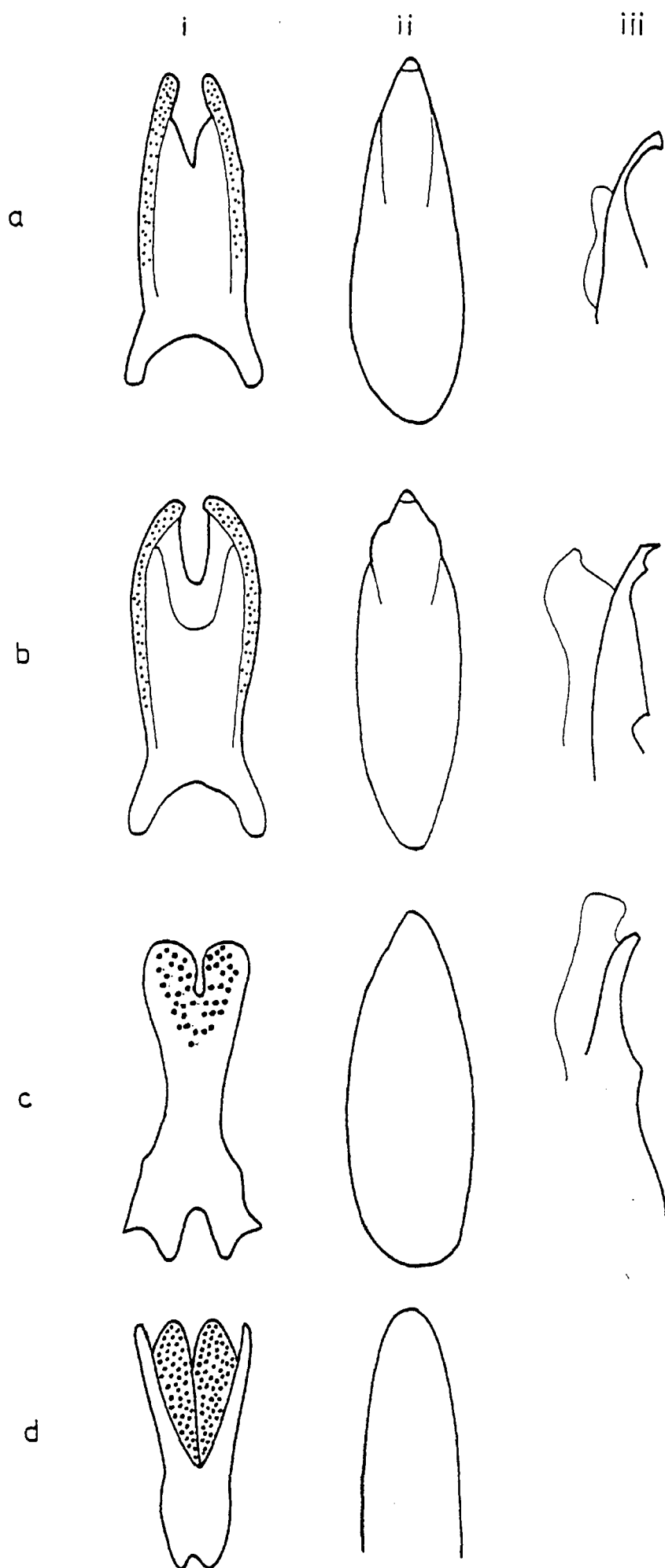
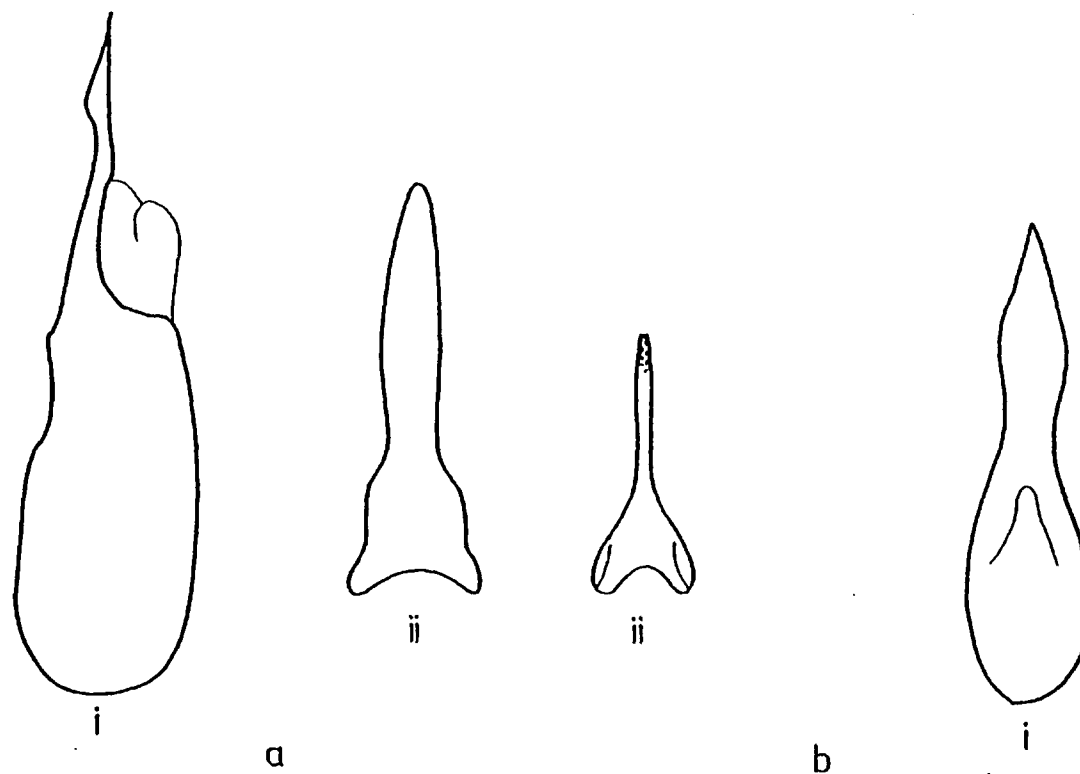
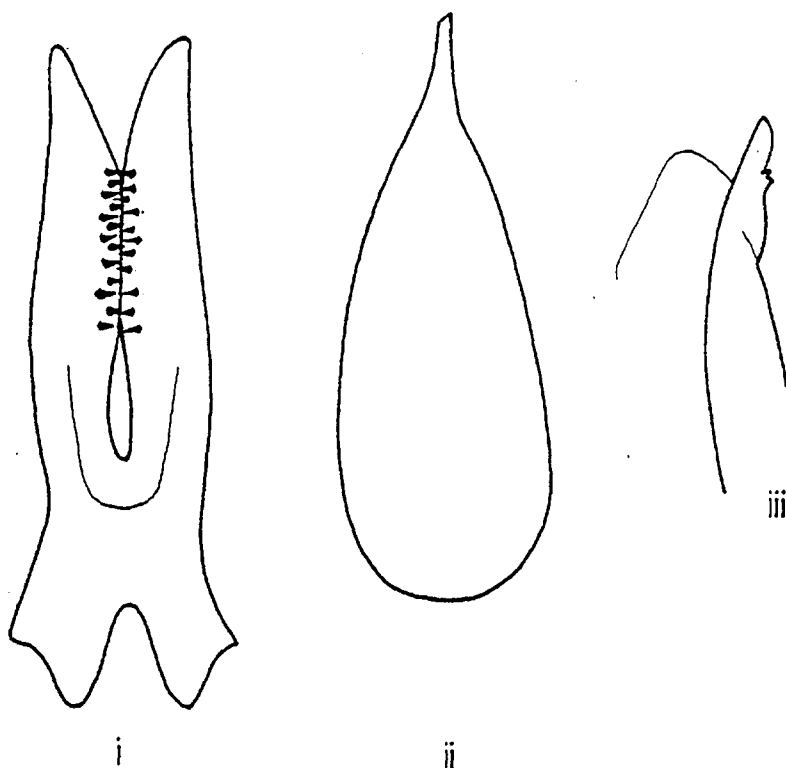


Fig.4.32 Male genitalia of Philonthus; a) P.sp.1, i. median lobe lateral view, ii. lateral lobe, b) P.nairobiensis, i. lateral lobe, ii. median lobe.



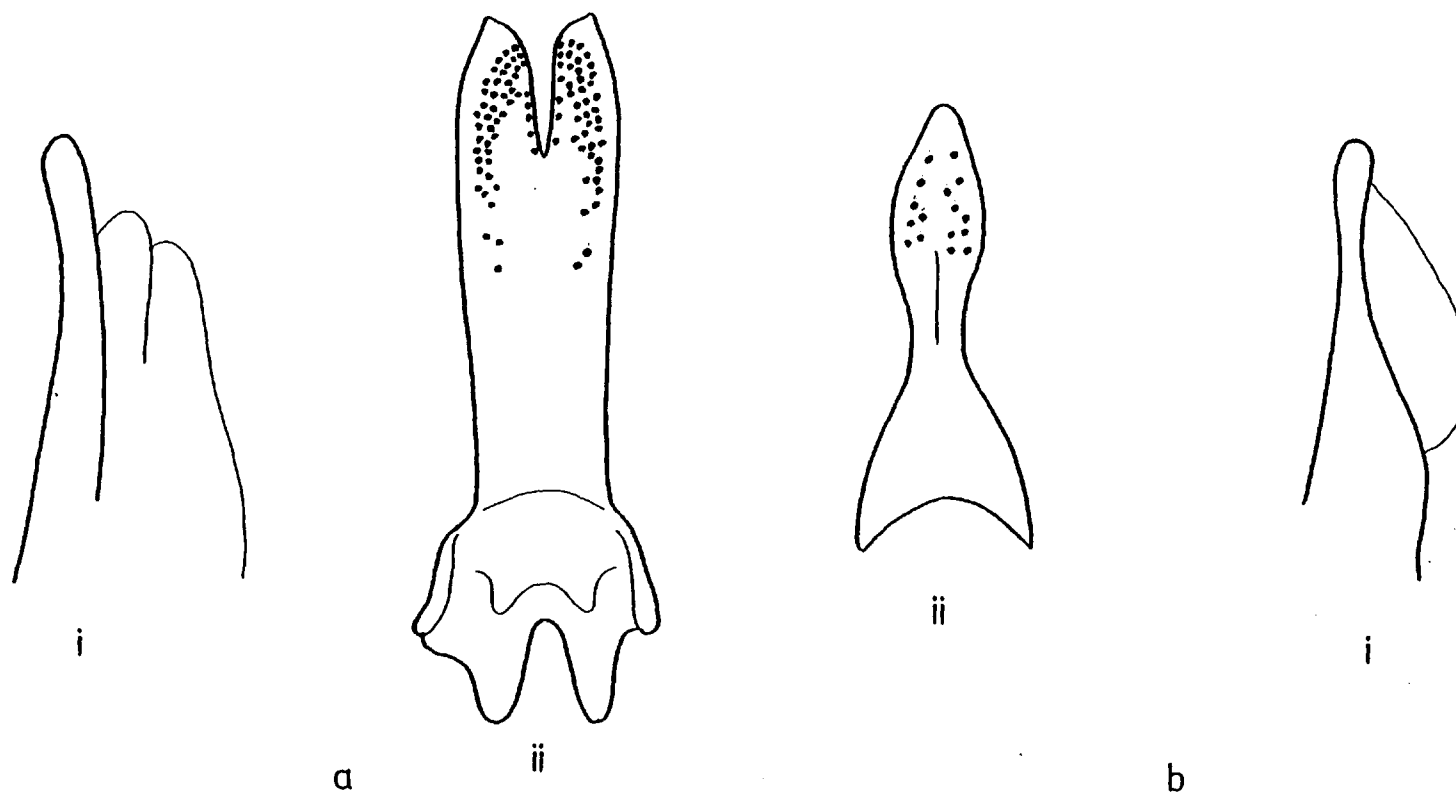
0.2mm

Fig.4.33 Male genitalia of Philonthus mongendensis, i. lateral lobe, ii. median lobe, iii. median lobe apex.



(i & iii) 0.2mm
(ii) 0.5mm

Fig.4.34 Male genitalia of Philonthus; i. median lobe apex, ii. lateral lobe, a) P.sp.2, b) P.tristichus.



0.2mm

Fig.4.35 Male genitalia of Philonthus; i. median lobe apex, ii. lateral lobe, a) P.triseriatus, b) P.dilucidus.

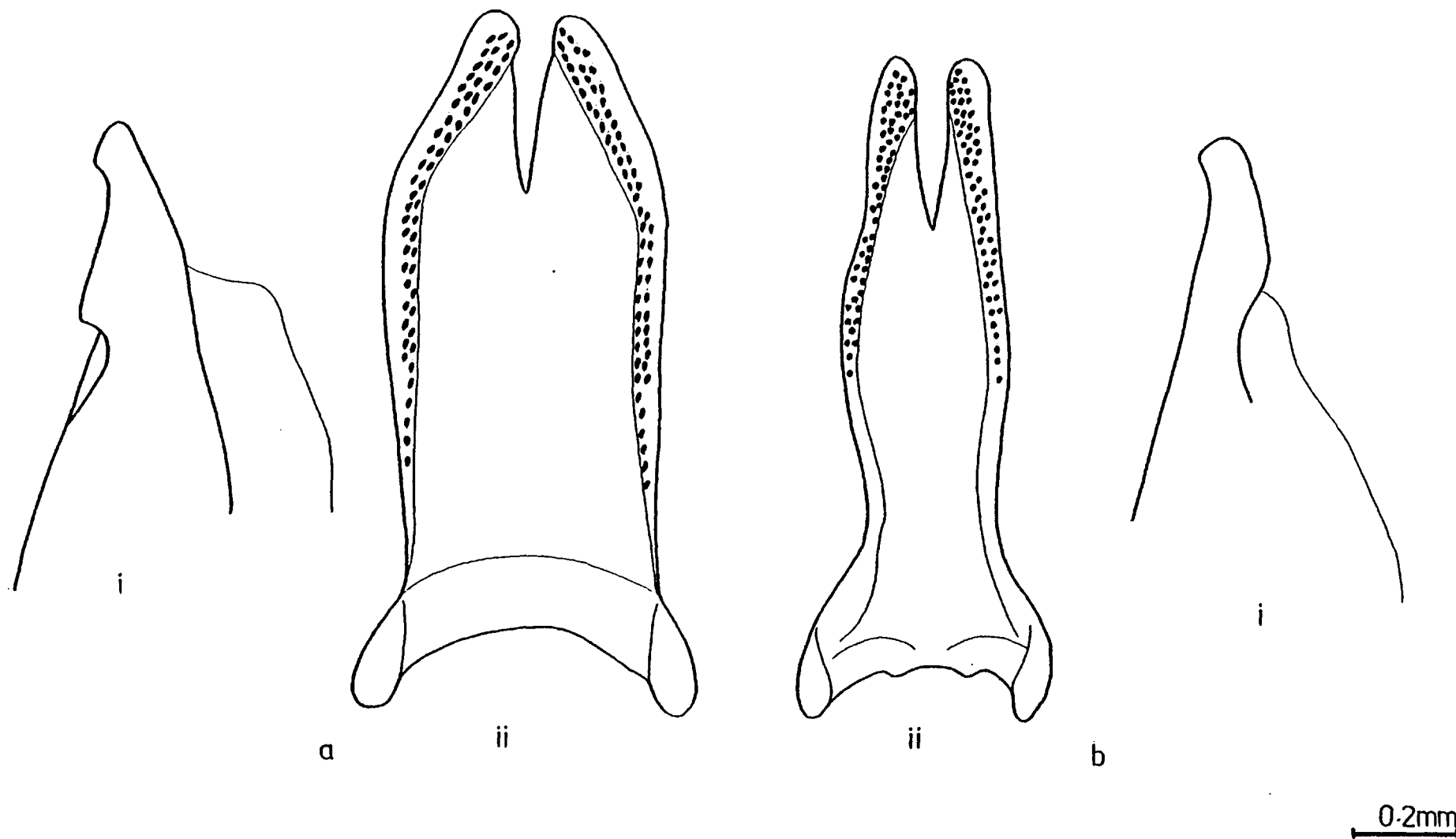


Fig.4.36 Male genitalia of Philonthus; i. median lobe, ii. median lobe apex, iii. lateral lobe, a) P.marginipennis, b) P.caperneri.

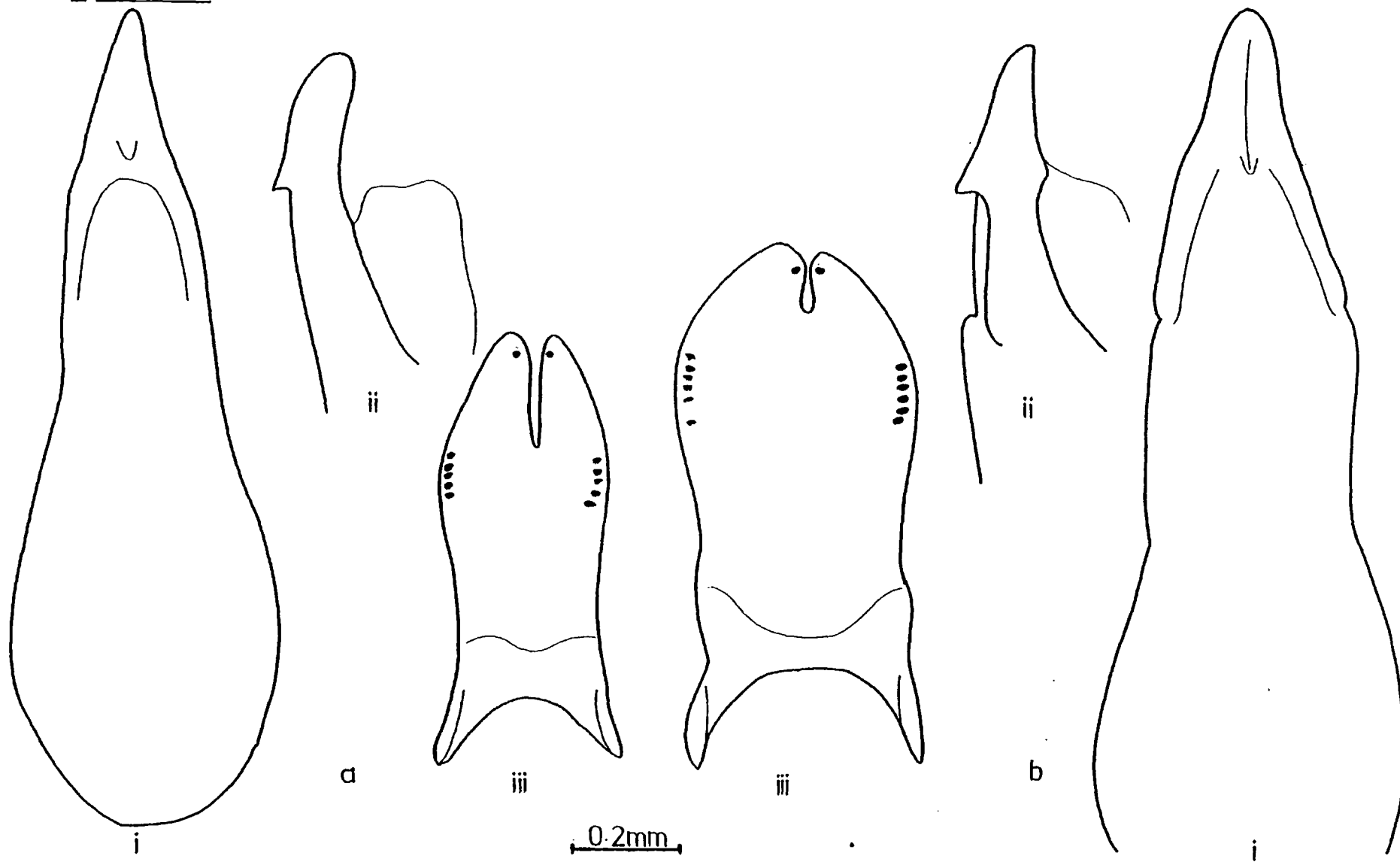


Fig.4.37 Male genitalia of Philonthus; i.median lobe, ii. median lobe apex, iii. lateral lobe, a) P.cinctus, b) P.parvicornis

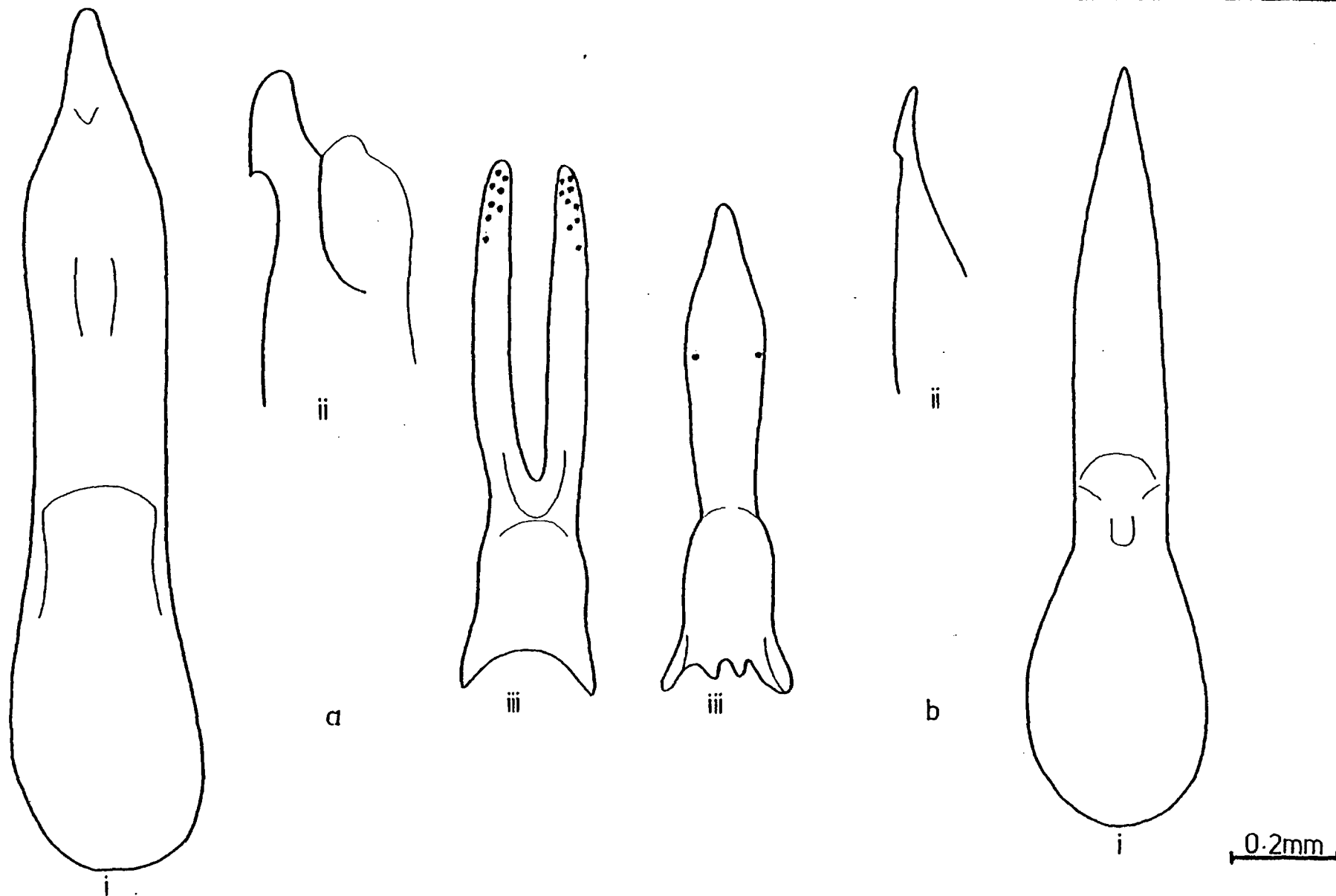
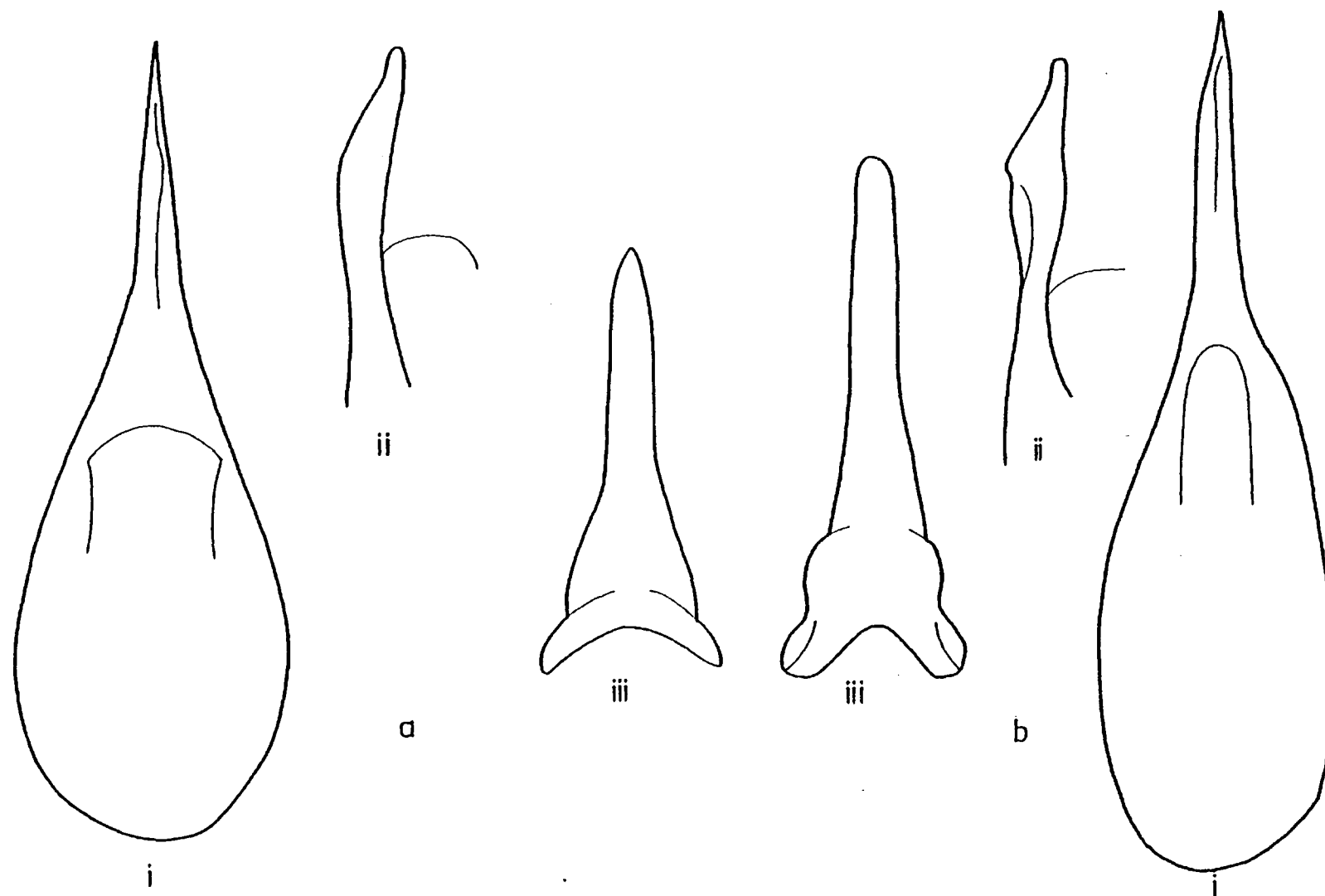


Fig.4.38 Male genitalia of Philonthus; i. median lobe, ii. median lobe apex, iii. lateral lobe, a) P.mivutamis,
b) P.stercorosus.



0.2mm

Similarly the following species exhibit very minor differences in external morphology while the male genitalia are very different (Fig. 4.39).

*P. discoideus Gravenhorst

P. negligens Tottenham

*P. neuter Tottenham

P. senegalensis Bernhauer

*P. testaceocinctus Bernhauer

*P. upuzius Tottenham

P. xanthoraphis Eppelsheim

The known habitats of all these species include cow, elephant and white rhinoceros dung.

Philonthus politus group.

P. addendus Sharp

P. politus (Linnaeus)

P. succicola Thomson

Distribution and Habitat

Details are given in Horion (1965).

P. addendus

North Palaearctic: north and central Europe.

P. politus

Holarctic: Iceland, North America, Tasmania, New Zealand, and Palaearctic.

P. succicola

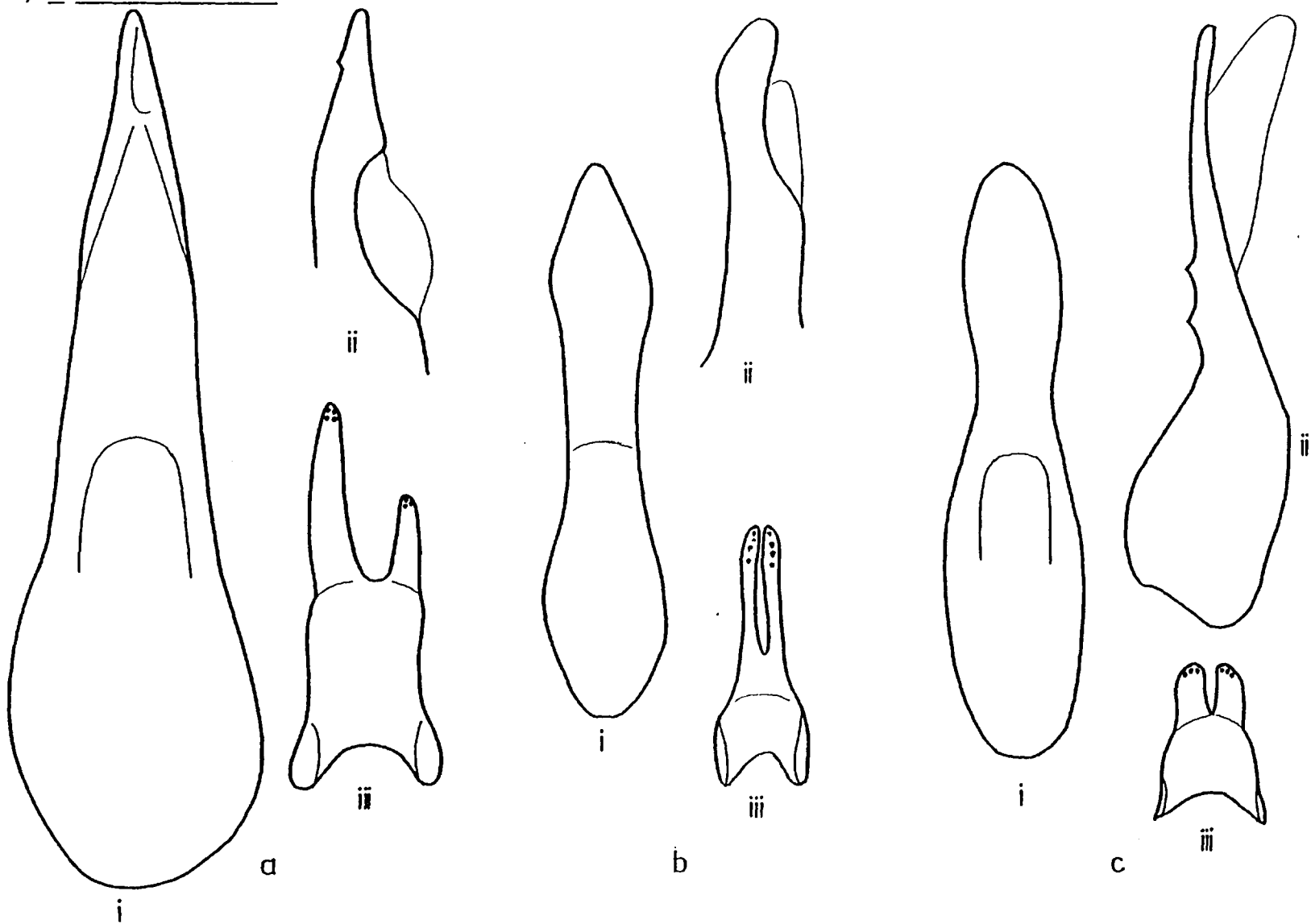
Palaearctic: Europe, Siberia, and north India.

The British distribution of the three species is very similar; P. addendus is more local, while P. politus is very common. All three species are very closely allied and are easily confused.

They occur in the same habitats of rotting vegetable matter, carrion

*species housed in BMNH.

Fig.4.39 Male genitalia of Philonthus; i. median lobe, ii. median lobe apex, iii. lateral lobe, a) P.neuter, b) P.discoideus, c) P.testaceocinctus.



0.2mm

and dung.

Secondary Sexual Characters

P. addendus (Fig. 4.40)

Sternite VIII: with central V-shaped emargination.

Median lobe: apically distinct, with pre-apical ridge in the mid-line.

Lateral lobe: 8-10 tooth-like peg setae arranged in two irregular columns at the apex of the lobe.

P. politus (Fig. 4.40)

Sternite VIII: with central V-shaped emargination.

Median lobe: apically distinct, with two pre-apical teeth close together.

Lateral lobe: with 40-50 small rounded peg setae arranged in two ill-defined columns towards centre of lobe.

P. succicola (Fig. 4.40)

Sternite VIII: with central V-shaped emargination.

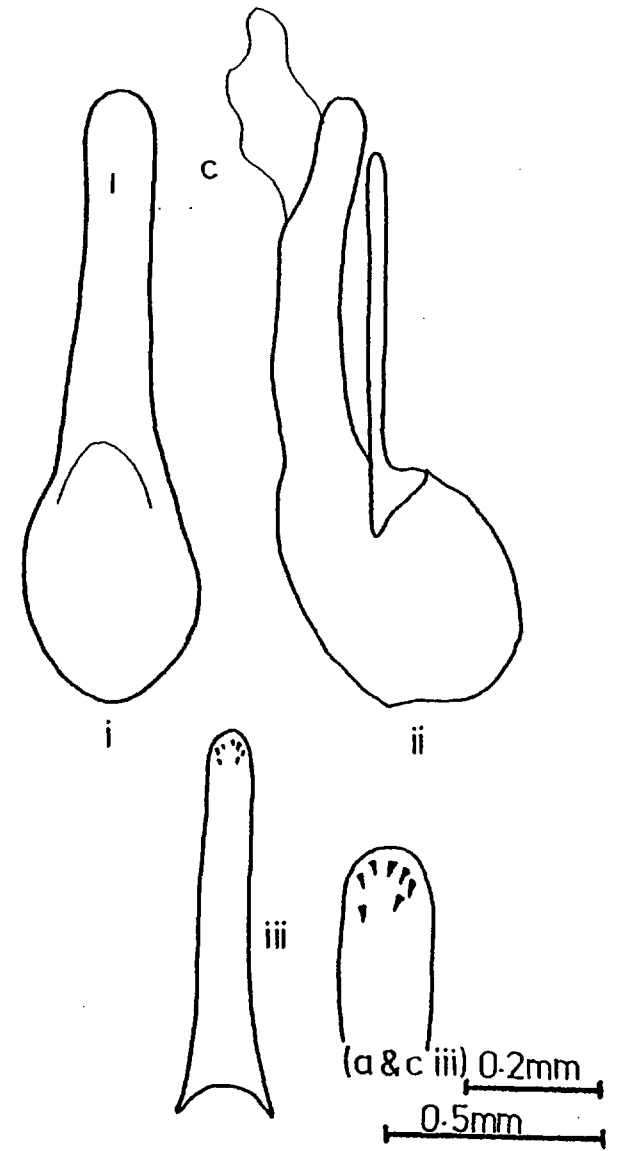
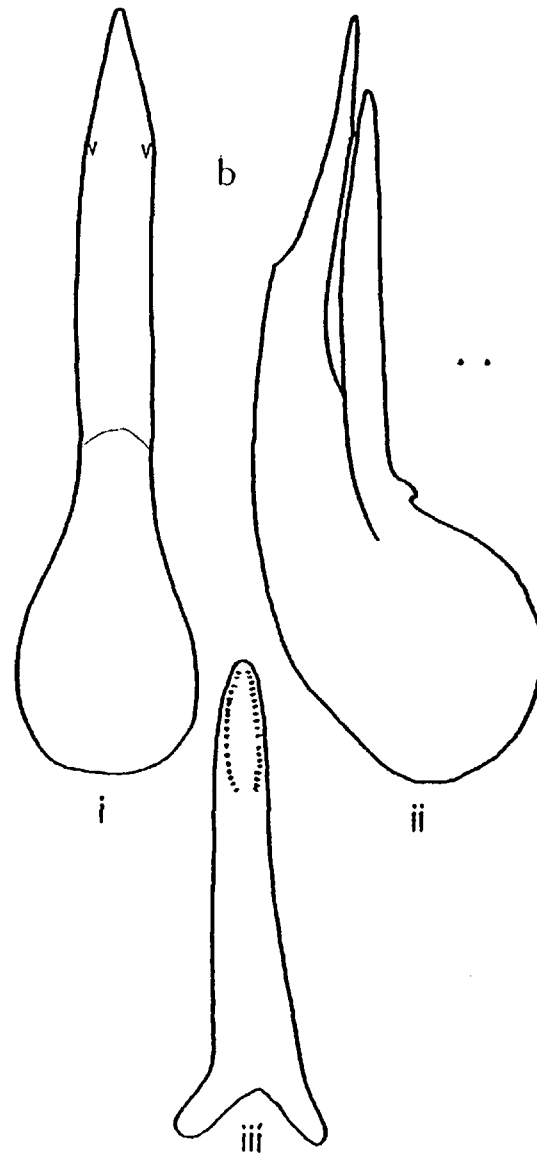
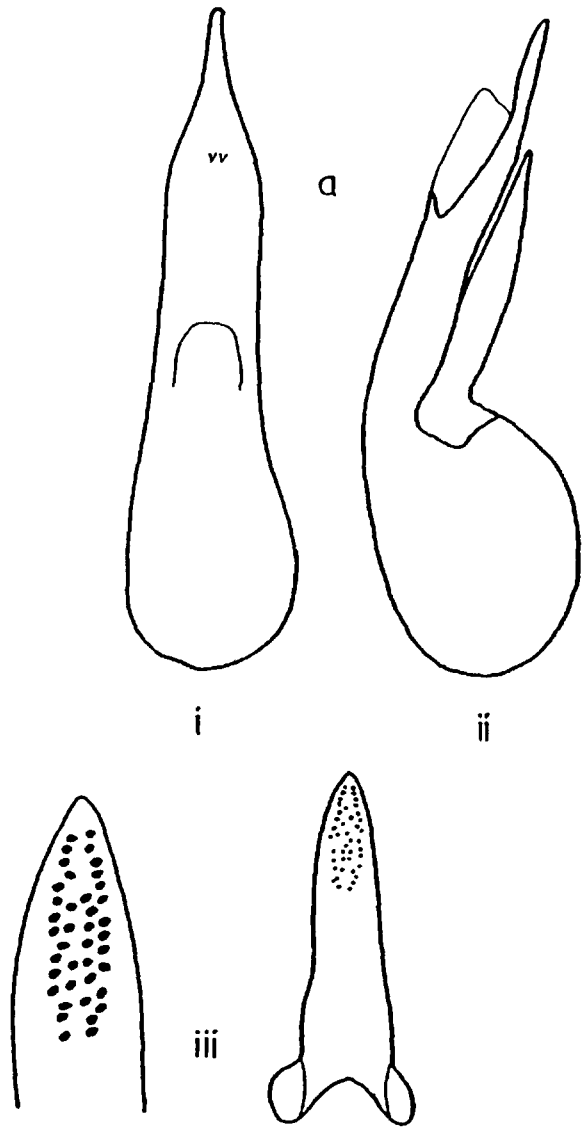
Median lobe: apically distinct with two pre-apical teeth at lateral margins.

Lateral lobe: 30-40 larger ovoid peg setae arranged in two well defined columns around the lateral edges of the lobe.

Variation

Nine male P. politus from a single population collected from Cheam, Surrey by Tottenham show the range of variation in the peg pattern from two reasonably defined columns of pegs with a narrow space between, to a mass of pegs without a regular pattern and without a central clear area. The numbers of pegs vary from 38-48. The lateral lobe shape varies in breadth and in the amount of apical tapering (Fig. 4.40). There is no indication of differences in peg arrangement outside the geographical range of P. succicola. Specimens from countries where P. politus

Fig.4.40 Male genitalia of Philonthus; i. median lobe dorsal view,
ii. median lobe lateral view, iii. lateral lobe,
a) P.politus, b) P.succicola, c) P.addendus.



is an introduced species, Tasmania, Chile, Azores and New Zealand are all comparable to Palaearctic specimens. Only one Canadian male exhibited a pattern which approached that of P. succicola with two clear columns of pegs converging at the posterior and anterior ends (Fig. 4.40). P. succicola is easily distinguished from P. politus by the shape of the lateral lobe, by the peg setae, which are ovoid and almost twice the size, and the peg pattern. Seven specimens from a single population collected from Addlestone, Surrey by Tottenham exhibit variation in peg number (from 13-19 in one column), in peg size (when there is a greater number of pegs their size decreases but still not to the size in P. politus). P. addendus is easily distinguished from P. politus and P. succicola by the spatulate apex of the median lobe, its pre-apical central ridge, and the tooth-like peg setae and peg pattern.

This is therefore a case of three syntopic species, exhibiting almost indistinguishable external morphology with very different peg patterns, and also with peg setae of all three species a different shape.

Philonthus sordidus Group

P. cephalotes (Gravenhorst)

P. nigriventris Thomson

P. parvus Sharp

P. pseudoparcus Brunne

P. sordidus (Gravenhorst)

Distribution and Habitat

Details are given in Horion (1965)

P. cephalotes

Holarctic: Europe, north Africa, Siberia, Iceland, north and central America.

P. nigriventris

North and central Europe, Scandinavia (not Denmark), Scotland and north England.

P. parvus

Japan, Australia, Europe: Elbe, Hamburg, Rheinland
Scandinavia.

P. pseudoparcus

Lauenburg: Oberelbe, Kastellaun: Hunsrück, Dibbersen:
Hamburg, Horst: Hamburg, Wildeshausen: Oldenburg.
" " Bronnoy Asker b. Oslo, Norway.
England.

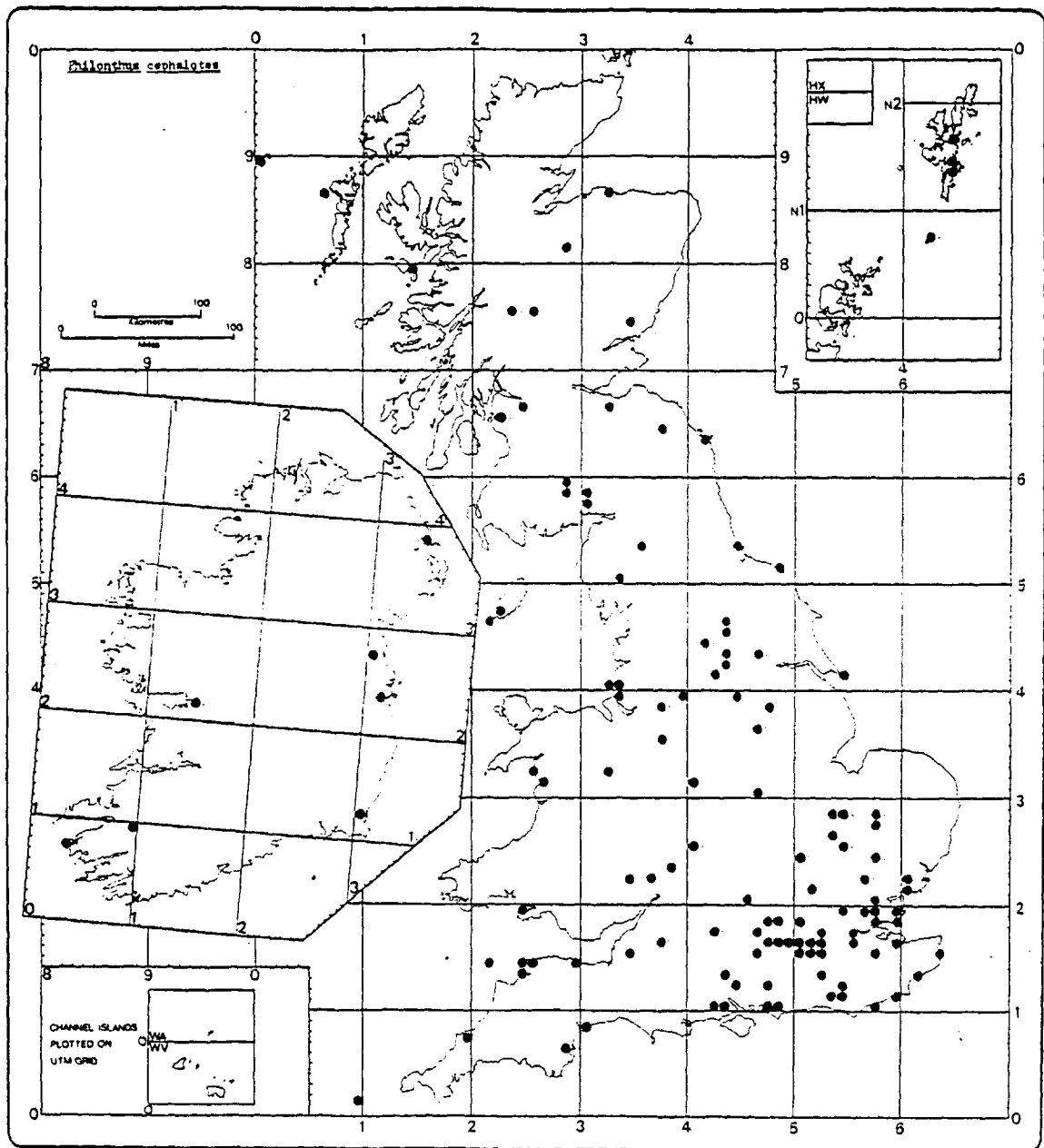
The British distribution of the P. sordidus group has been studied in detail using records from extensive collections in the BMNH and Manchester Museum (although this has been by no means exhaustive). Maps:1-5

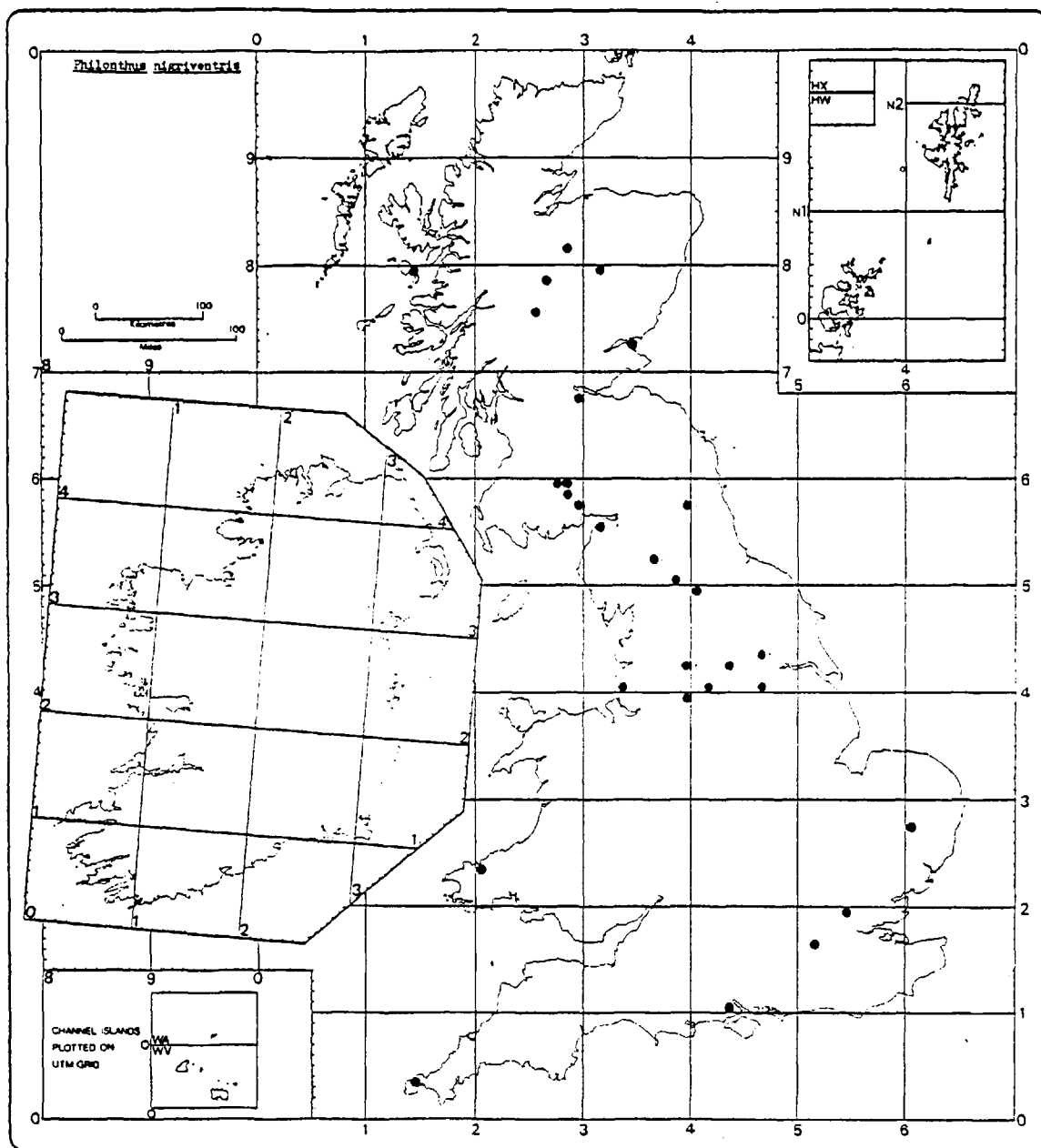
The distribution of P. sordidus and P. cephalotes are very similar. They are frequently found syntopically in synanthropic habitats, P. cephalotes being more common in habitats in a later stage of putrefaction as well as nests, dung etc.

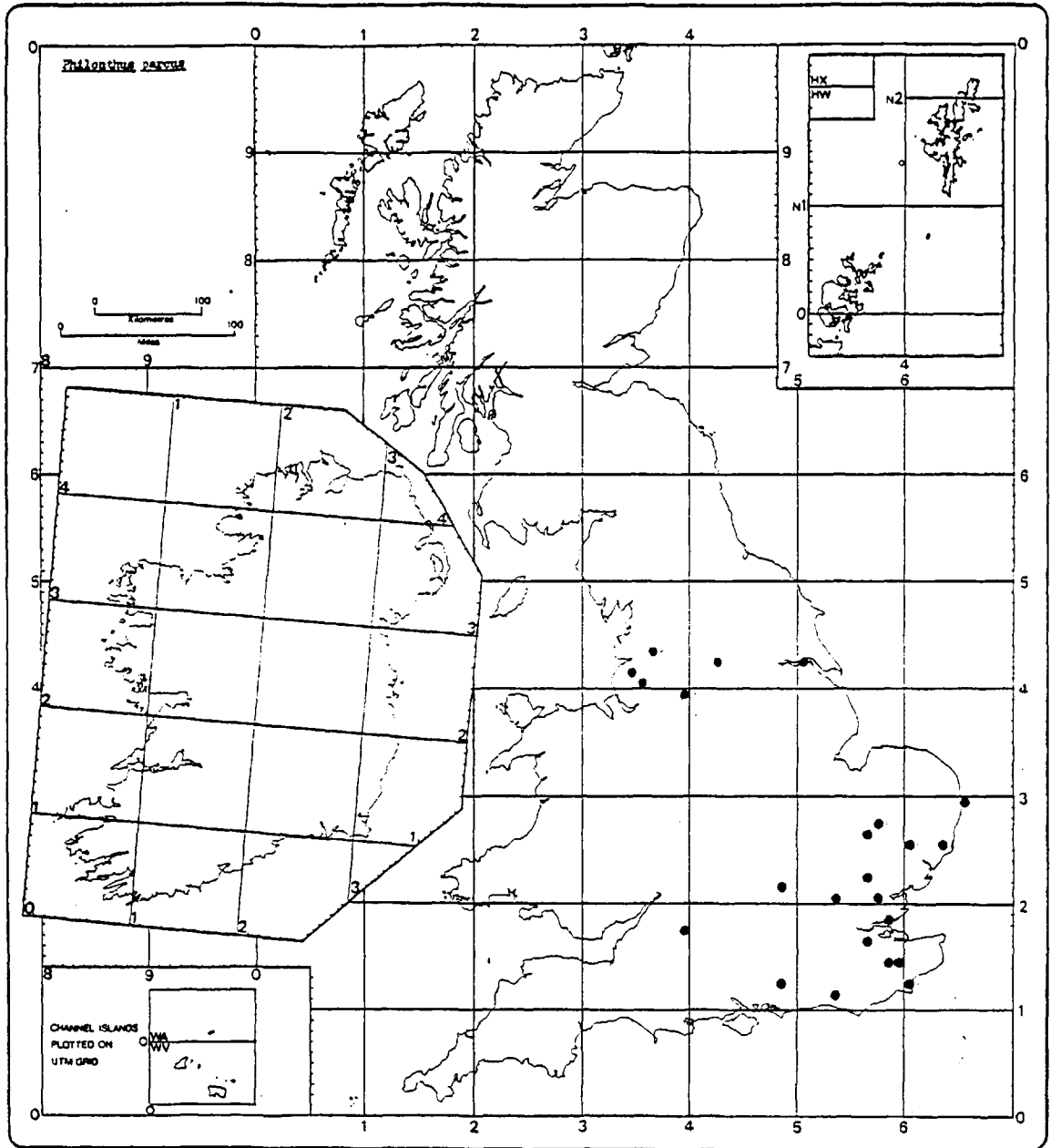
P. nigriventris is probably rarely syntopic with any other species of the group. It has a more northerly and local distribution and prefers a more sandy habitat such as light pine forests or even dead birds and mammals. P. parvus has an isolated distribution, often being associated with hen houses (in chicken dung and grain) but is sometimes syntopic with the other species of the group (Section 7).

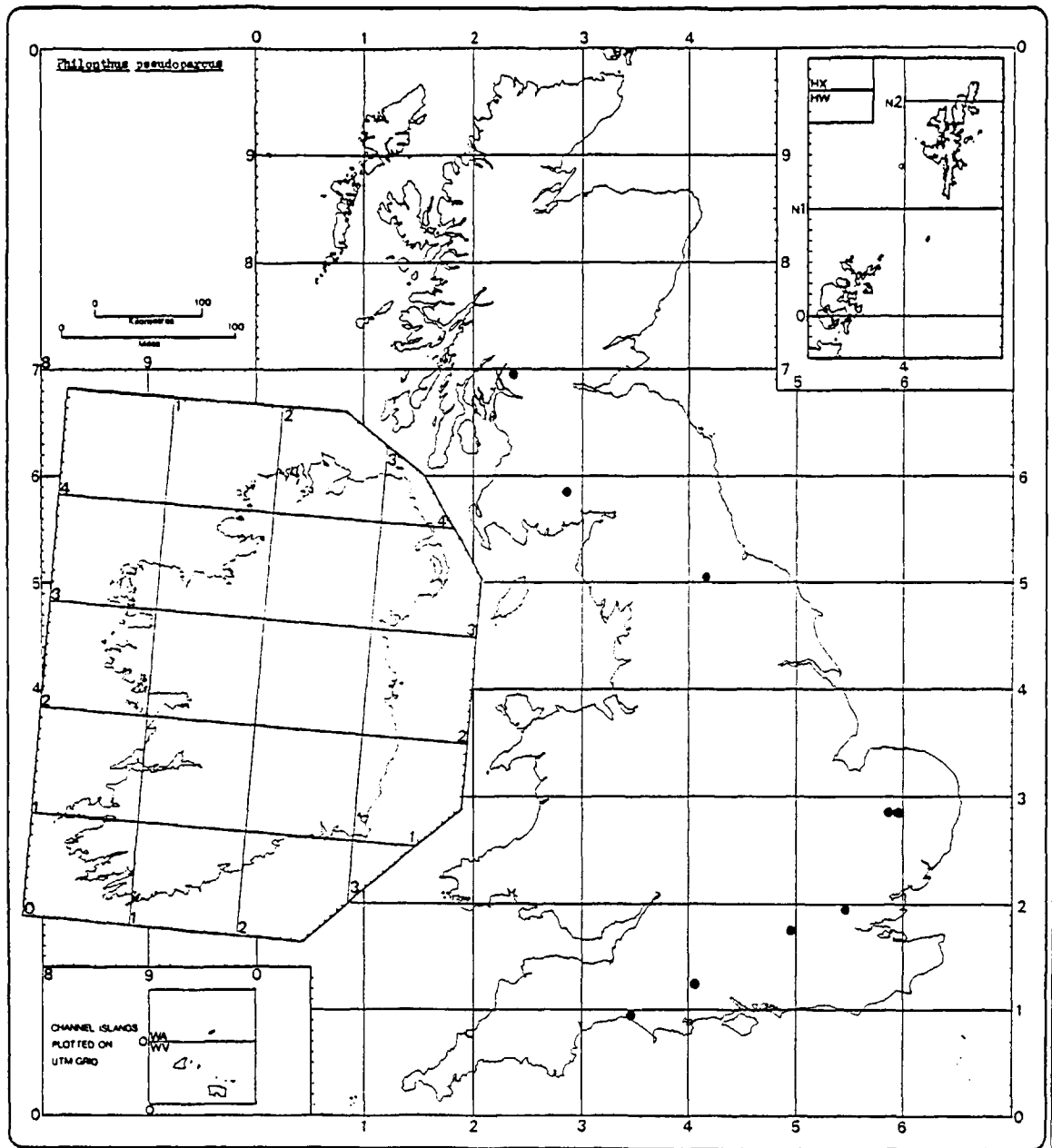
P. pseudoparcus has only recently been discovered in Britain. It was first described by Brunne (1976) from locations in Germany. It has subsequently been discovered amongst British specimens of P. sordidus in the BMNH and it is likely that this will be the case in many collections. It seems to be typical of more non-synanthropic situations than P. sordidus, i.e. forests (in deer and cow dung) and in fungi. Whether it is syntopic with P. sordidus or P. cephalotes remains unknown although it is probable it may sometimes be so.

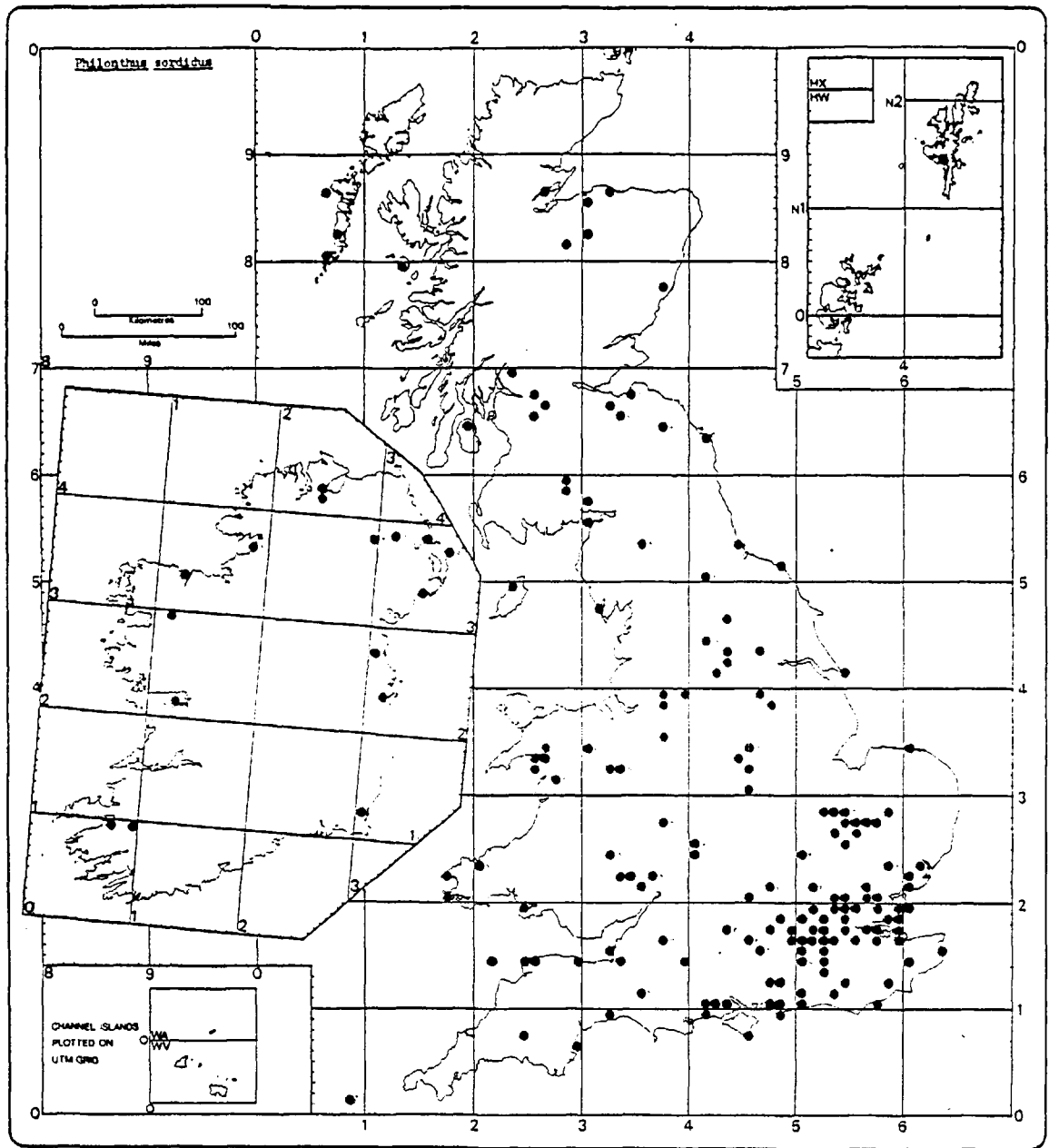
Map 1. Distribution of Philonthus cephalotes in the British Isles.





Map 3. Distribution of Philonthus parvus in the British Isles.

Map 4. Distribution of Philonthus pseudoparcus in the British Isles.

Map 5. Distribution of Philonthus sordidus in the British Isles.

Secondary Sexual Characters

The male secondary sexual characters are typical of the genus, with the evaginated posterior margin of the eighth sternite, the form of the median lobe apex, lateral lobe shape and peg pattern. (Plates 4.1-4.5). It is significant that the greatest difference in pattern of the lateral lobe peg setae occurs in P. cephalotes which is the only one of the species which can be found truly syntopically with another (P. sordidus). The peg patterns of the other species, although specifically distinct are very much of the P. sordidus type.

Variation

There is much variation in the precise position of the lateral lobe peg setae, and in their numbers; however, this does not alter the overall character of the pattern which is of the greatest importance. Four specimens of P. sordidus collected at the same time from one locality showed a variation in total peg number from 18-27. Three P. cephalotes, also from the same location at the same time (i.e. syntopic), varied in peg number from 19-22. There is also minor variation in the shape and size of the lateral lobe and median lobe apex.

Function

Refer to the mating behaviour in Philonthus species (Section 5.2.1-7) and relationships in P. sordidus-group are discussed in Section 7.

GABRIUS Stephens

- G. bishopi Sharp
- G. keysianus Sharp
- G. nigritulus Gravenhorst
- G. pennatus Sharp
- G. piliger Mulsant & Rey
- G. subnigritulus Reitt.
- G. trossulus (Nordm.)
- G. velox Sharp

Plate.4.3. Scanning electron micrographs of the median lobe of the male genitalia of Philonthus sordidus.

a) latero-dorsal view (x 120)

b) latero-dorsal view of setae around apex (x 660)

c) dorsal view apex (x 300)

d) dorsal view apex (x 1200)

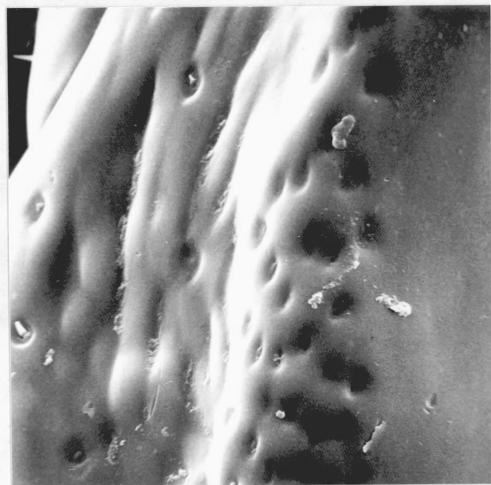
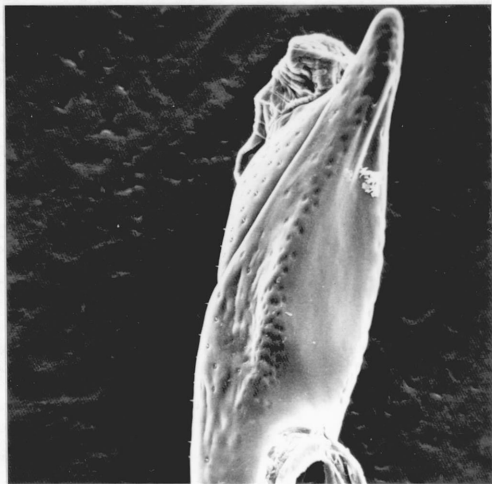


Plate. 4.4. Scanning electron micrographs of the median lobe apex and everted internal sac of Philonthus sordidus.

- a) dorsal view median lobe apex (x 300)
- b) dorsal view median lobe apex and everted internal sac (x 300)
- c) dorsal view median lobe apex and part of everted internal sac (x 600)
- d) dorsal view median lobe apex and part of everted internal sac (x 1200)
- e) internal sac (x 1200)
- f) flagellum of internal sac (x 600)

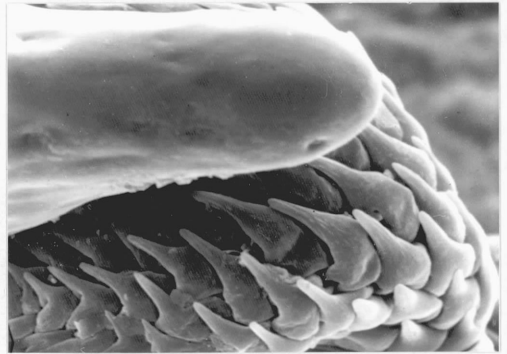
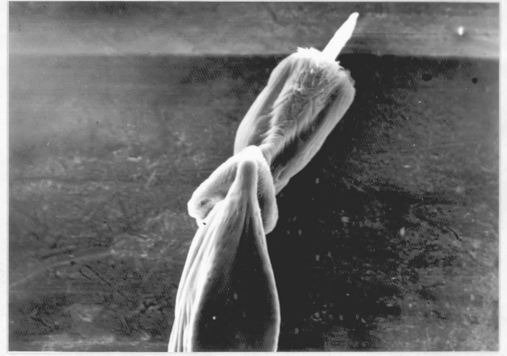
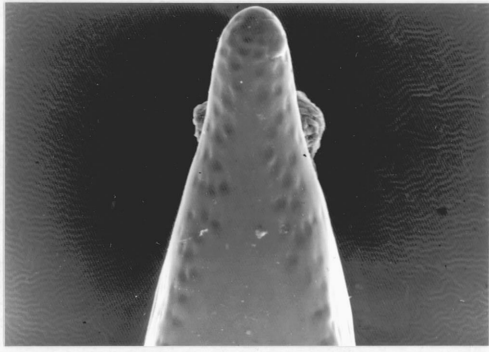
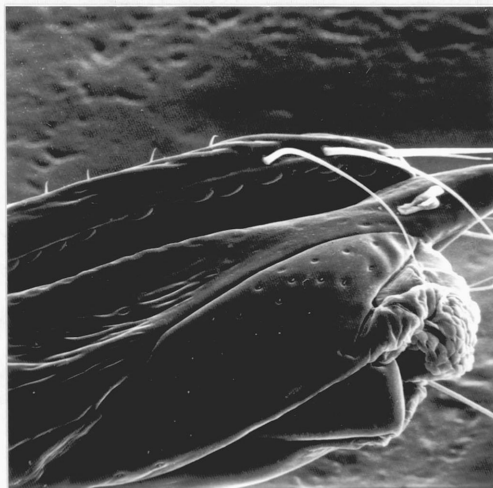
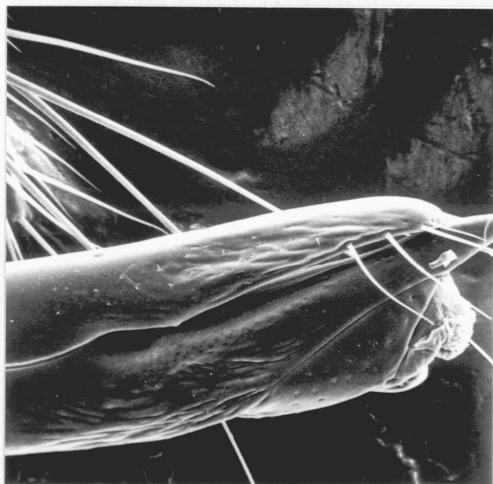
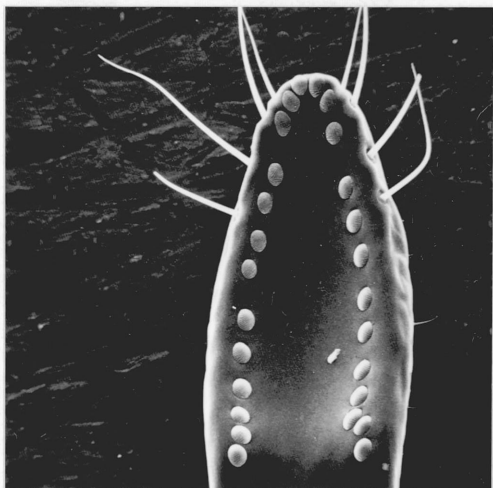
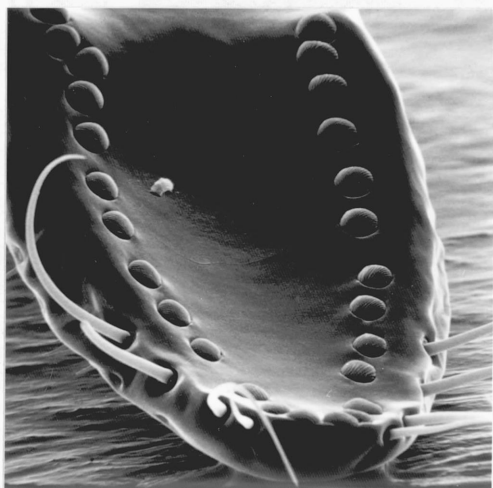
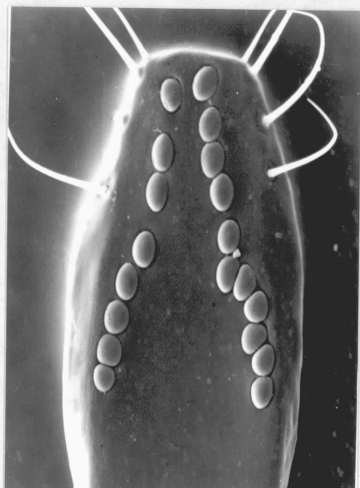
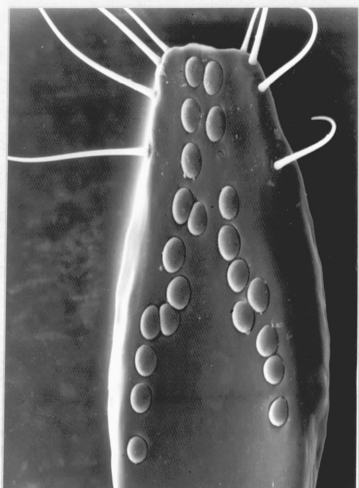


Plate.4.5. Scanning electron micrographs of the male genitalia of
Philonthus sordidus and P.cephalotes.

- a) Ventral view of lateral lobe and peg setae of P.cephalotes
(x 300)
- b) Ventral view of lateral lobe and peg setae of P.cephalotes
(x 300)
- c) Postero-ventral view of lateral lobe and peg setae of
P.sordidus (x 396)
- d) Ventral view of lateral lobe and peg setae of P.sordidus
(x 168)
- e) Lateral view of median and lateral lobe of P.sordidus
(x 160)
- f) Dorso-lateral view of median and lateral lobe of
P.sordidus (x 180)



The Gabrius nigritulus group is very large, many species being previously confused under one name. The external morphology of all the species is extremely similar. Females are particularly difficult to distinguish, although the male genitalia were found to afford good specific characters (Coiffait, 1951).

Many new species have been named on the basis of male genital characters alone. In the case of the species named above the differences between them are substantial; however, in other cases species have been named on the basis of minor differences in genitalia in isolated populations. Such differences could be accounted for by geographical variation.

Distribution and Habitat

Distributional data for species in the G. nigritulus group is very incomplete owing to the previous confusion under a single species name.

G. bishopi

West and central Europe.

G. keysianus

West Europe. Not east of Holland or Belgium.

G. nigritulus

Palaeartic. India, Ceylon, Australia, north and south America.

G. pennatus

Europe and north Africa; Asia Minor; Caucasus.

G. piliger

South Palaeartic: central and southern Europe; Caucasus;

Asia Minor; south Siberia; north to south Sweden.

G. subnigritulus

North palaeartic: north and central Europe. Sporadic

distribution in mountains in south east Europe; Siberia.

G. trossulus

North and central Europe; Iceland.

G. velox

North and central Europe, probably also in southern Europe.

All eight species occur in Britain, other species in the group do not. G. nigrutilus, G. pennatus and G. subnigrutilus are common and widely distributed all over Britain. G. piliger and G. trossulus also have a wide distribution but are local in occurrence. The distribution of G. bishopi, based on specimens in the BMNH, is from Cambridgeshire to Scotland and of local occurrence. G. velox has a localised south-eastern and G. keysianus a localised southern distribution.

The habitats of all the species are similar; in rotting vegetation, and fungus, compost, dung and carrion. G. pennatus, G. trossulus and G. keysianus have a preference for damp situations. G. velox and G. subnigrutilus are moisture-loving species found on sea and pond shores, marshy places and in wet moss and sphagnum.

Secondary Sexual Characters

Sternite VIII: (Figs. 4.41-4.48)

Differences occur in the shape of the central triangular emargination of the posterior border of the sternite.

<u>G. piliger</u>	- absent
<u>G. velox</u>	- deep
<u>G. trossulus</u>	- deep
<u>G. pennatus</u>	- deep
<u>G. nigrutilus</u>	- less deep than <u>G. velox</u>
<u>G. keysianus</u>	- as <u>G. nigrutilus</u> but rounded
<u>G. bishopi</u>	- very deep
<u>G. subnigrutilus</u>	- very deep.

Median lobe: (Figs. 4.41-4.48)

The apex of the median lobe is characteristic for each species, with a ventral 3-dimensional development which is asymmetrical in some species.

Lateral lobe: (Figs. 4.41-4.48)

The lateral lobes fall into types, entire as in G. piliger and G. trossulus, or bifid with differences in the V or U-shaped separation of lobes between species.

In those species with an entire lateral lobe, peg setae occur on the surface facing the median lobe. When the lateral lobe is bifid, peg setae are borne on the tip of each lobe, facing the dorsal surface of the median lobe.

G. pennatus is distinct from the other species in having tooth-like peg setae.

Variation

It is possible that there is some geographical variation in the apex of the median lobe.

Some new species have been named on the basis of slight differences in genital characters, which could be accounted for by geographical variation (Bordoni, 1973).

G. sexualis Smetana from Italy is very similar to G. pennatus.

G. gagliardi Gridelli from Italy is very similar to G. keysianus.

G. mengensis Smetana from north-west Spain is very similar to G. gagliardi.

G. ravasinii Gridelli from Italy is very similar to G. nigritulus.

G. toxotes Joy (from France, Belgium, Dalmatia and Transylvania) is very near to G. subnigritulus.

G. mauretanicus Peyer (G. primigenius Joy) is very near to G. velox.

G. raubali Smetana (Caucasus) is very near to G. nigritulus (Smetana, 1962).

G. heres Smetana (Canary Is.) is very near to G. nigritulus (Smetana, 1962)

There also seems to be intraspecific variation in the numbers of pegs on each lobe. G. nigritulus has 2, G. keysianus 3, G. subnigritulus 2 or 3, G. bishopi and G. velox 3 or 4, and G. pennatus has 3 or 4 tooth-like pegs.

Fig. 4.41 Male genitalia of Gabrius nigritulus; a) median lobe ventral view, b) median lobe dorsal view c) median lobe lateral view, d) sternite VIII, e) lateral lobe f) peg setae on lateral lobe.

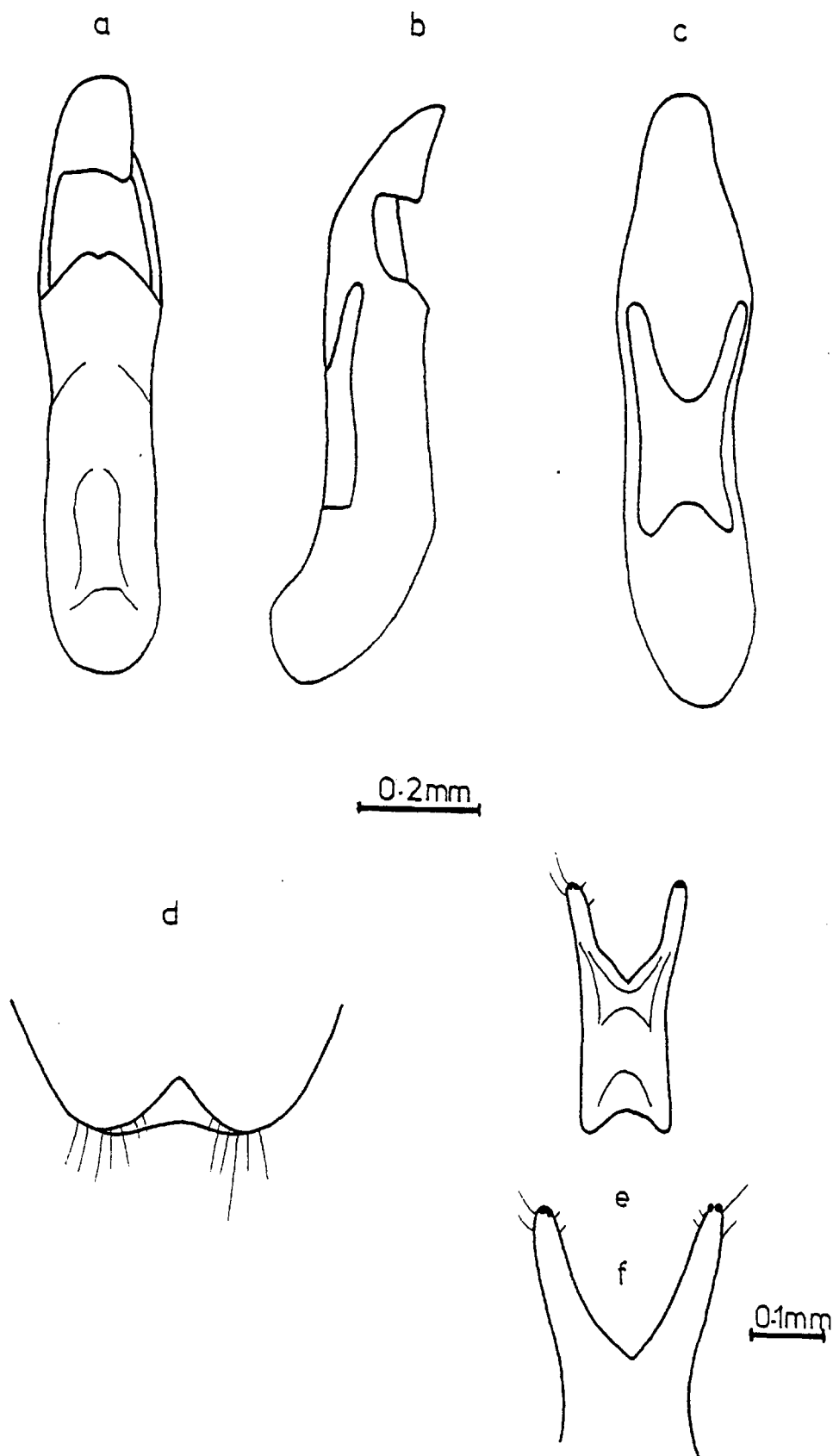


Fig.4.42 Male genitalia of Gabrius bishopi; a) median lobe ventral view, b) median lobe dorsal view, c) median lobe lateral view, d) sternite VIII, e) lateral lobe, f) peg setae on lateral lobe.

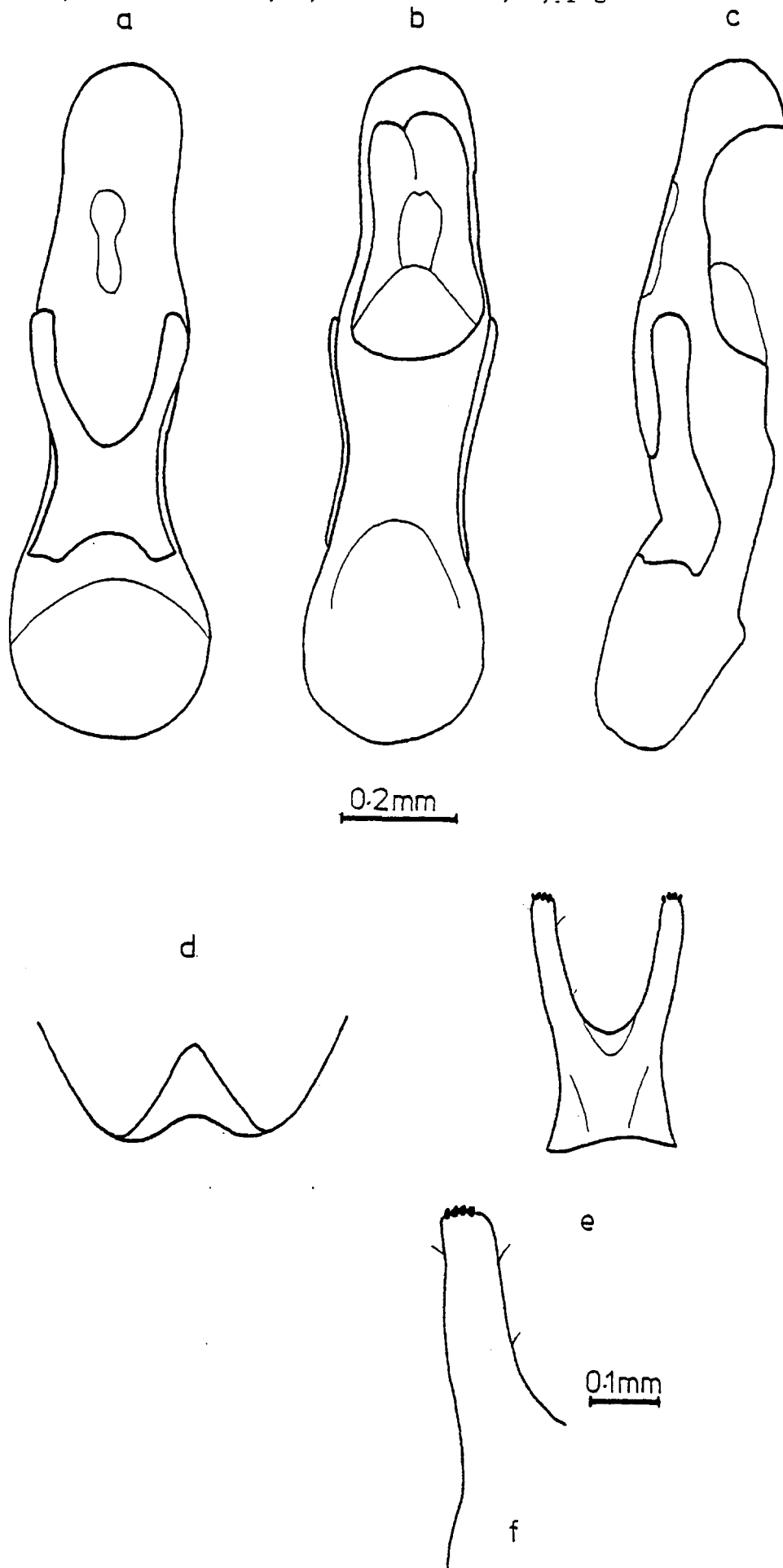


Fig.4.43 Male genitalia of Gabrius keysianus; a) median lobe ventral view, b) median lobe dorsal view, c) median lobe lateral view, d) sternite VIII, e) lateral lobe, f) peg setae on lateral lobe.

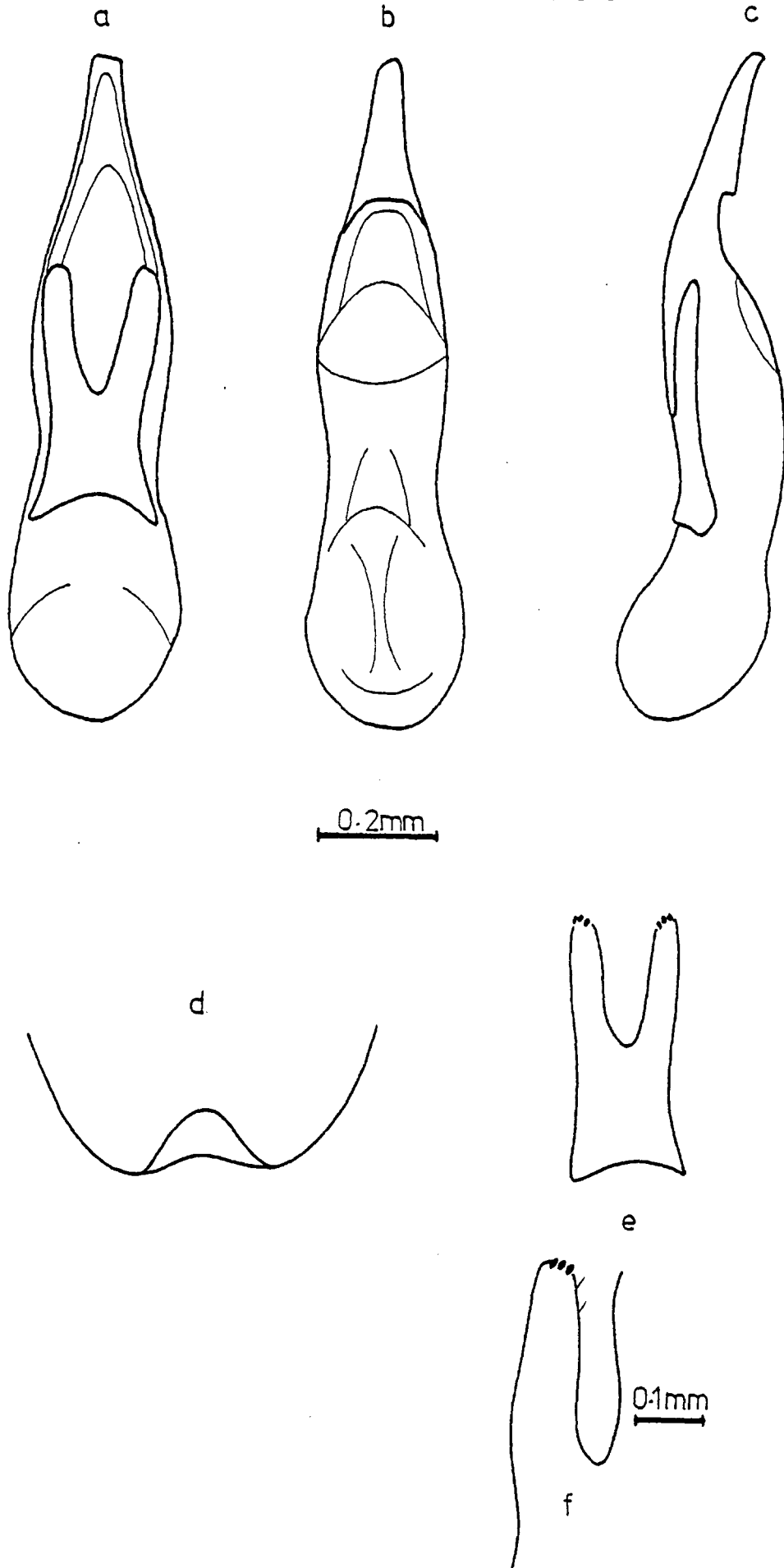
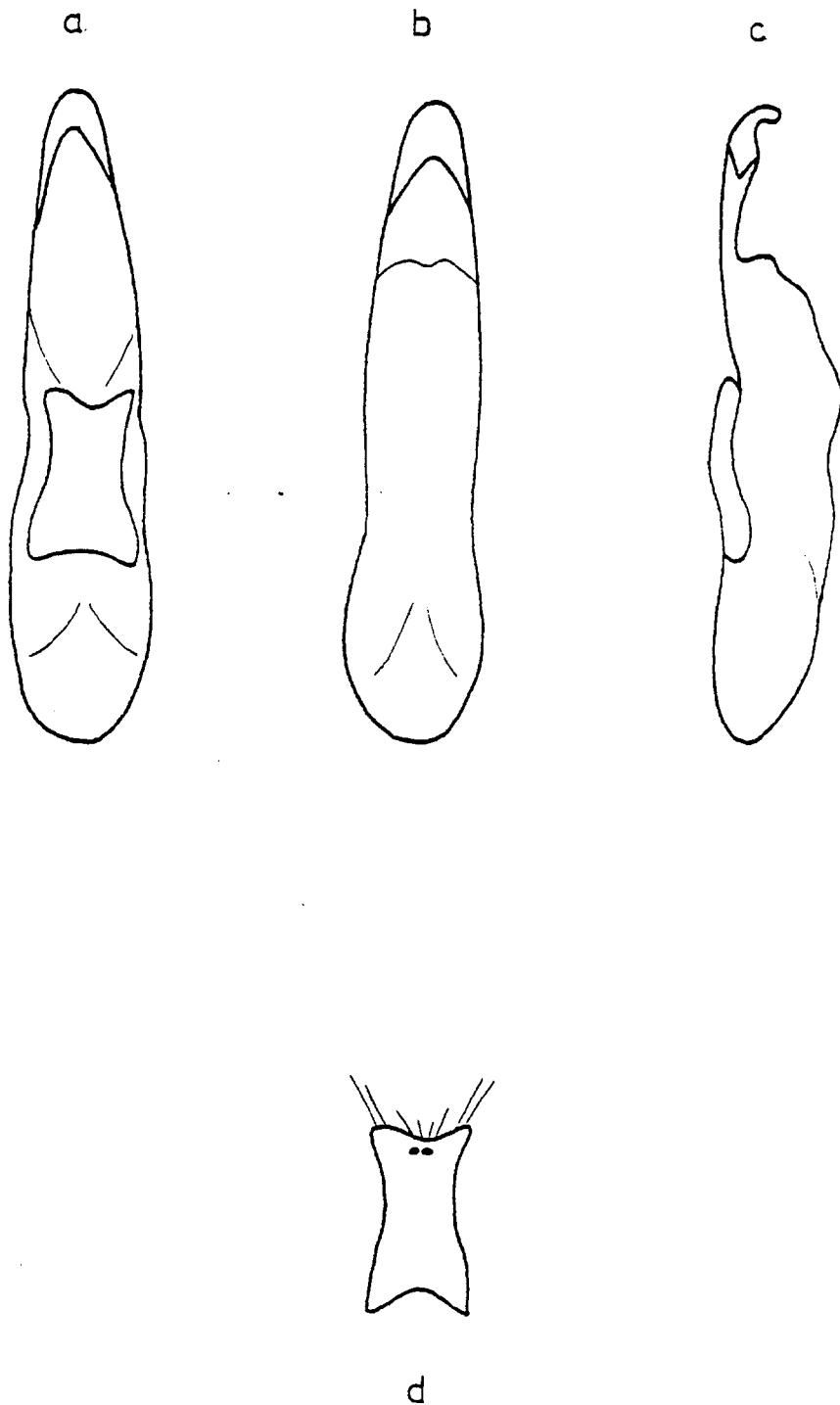


Fig.4.44 Male genitalia of Gabrius piliger; a) median lobe ventral view,
b) median lobe dorsal view, c) median lobe lateral view,
d) lateral lobe.



0-2mm

Fig.4.45 Male genitalia of Gabrius velox; a) median lobe ventral view, b) median lobe dorsal view, c) median lobe lateral view, d) sternite VIII, e) lateral lobe, f) peg setae on lateral lobe.

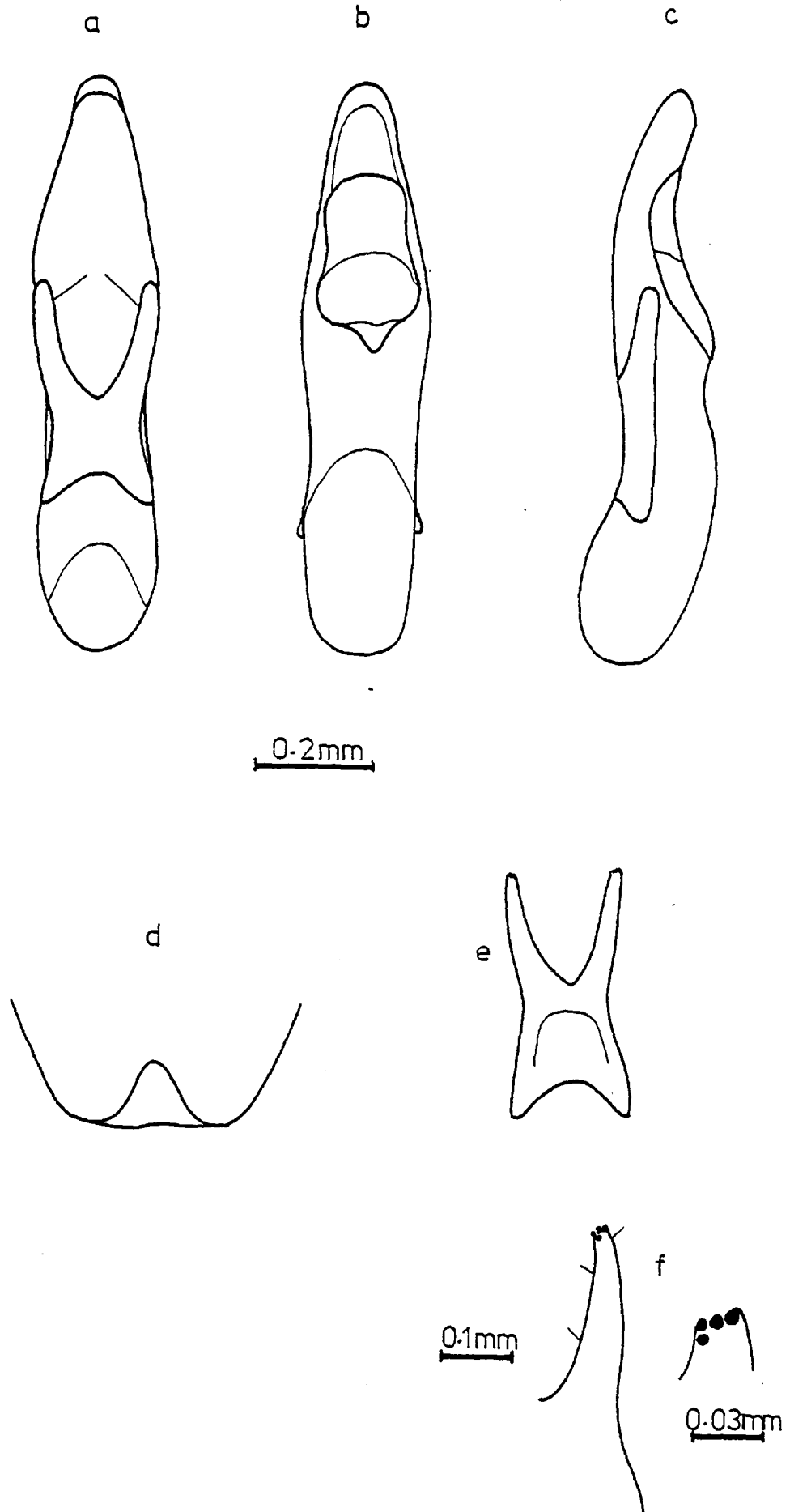


Fig.4.46 Male genitalia of Gabrius subnigritulus; a) median lobe ventral view, b) median lobe dorsal view, c) median lobe lateral view, d) sternite VIII, e) lateral lobe, f) peg setae on lateral lobe.

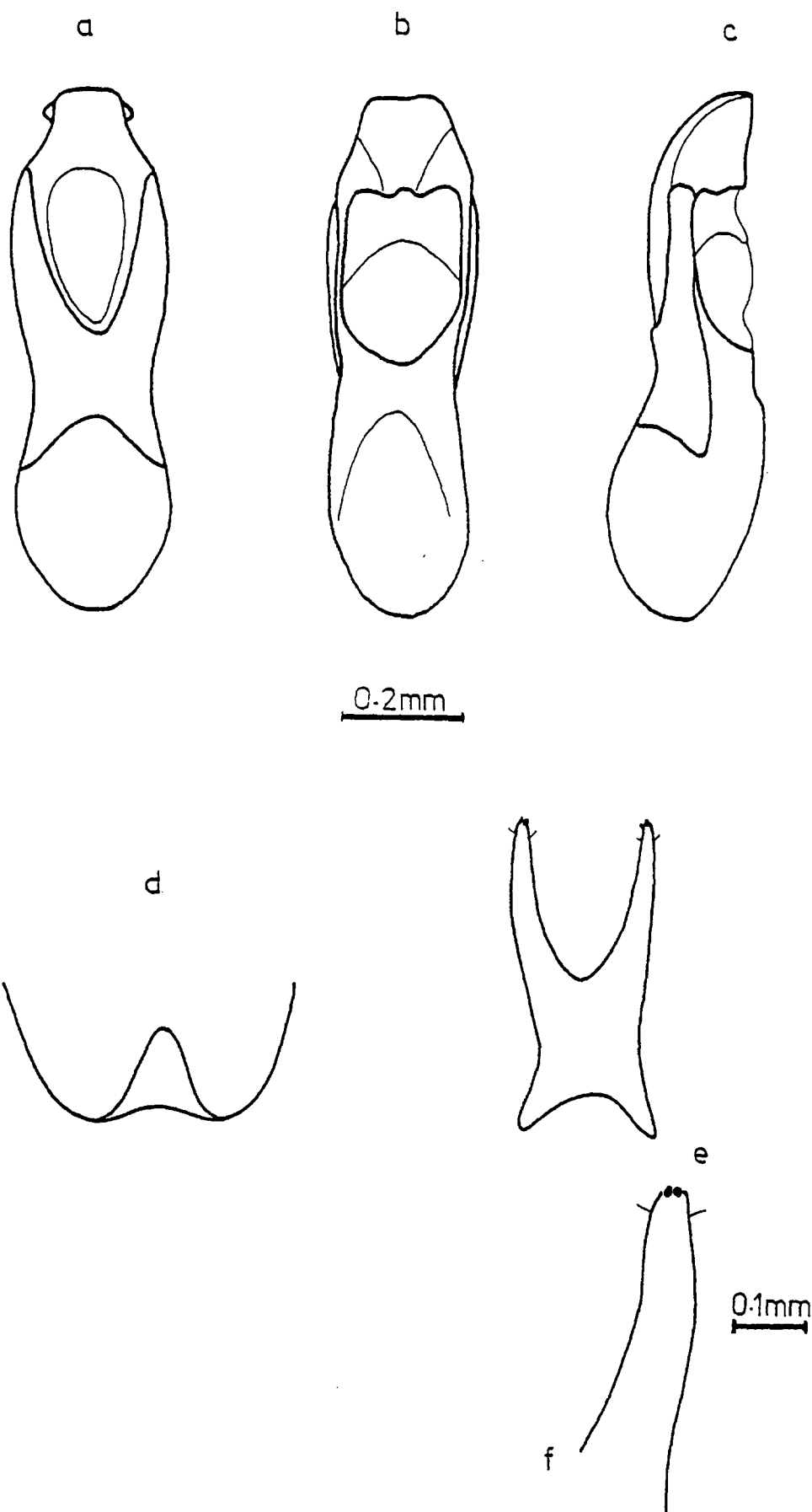


Fig.4.47 Male genitalia of Gabrius pennatus; a) median lobe ventral view, b) median lobe dorsal view, c) median lobe lateral view, d) sternite VIII, e) lateral lobe, f) peg setae on lateral lobe.

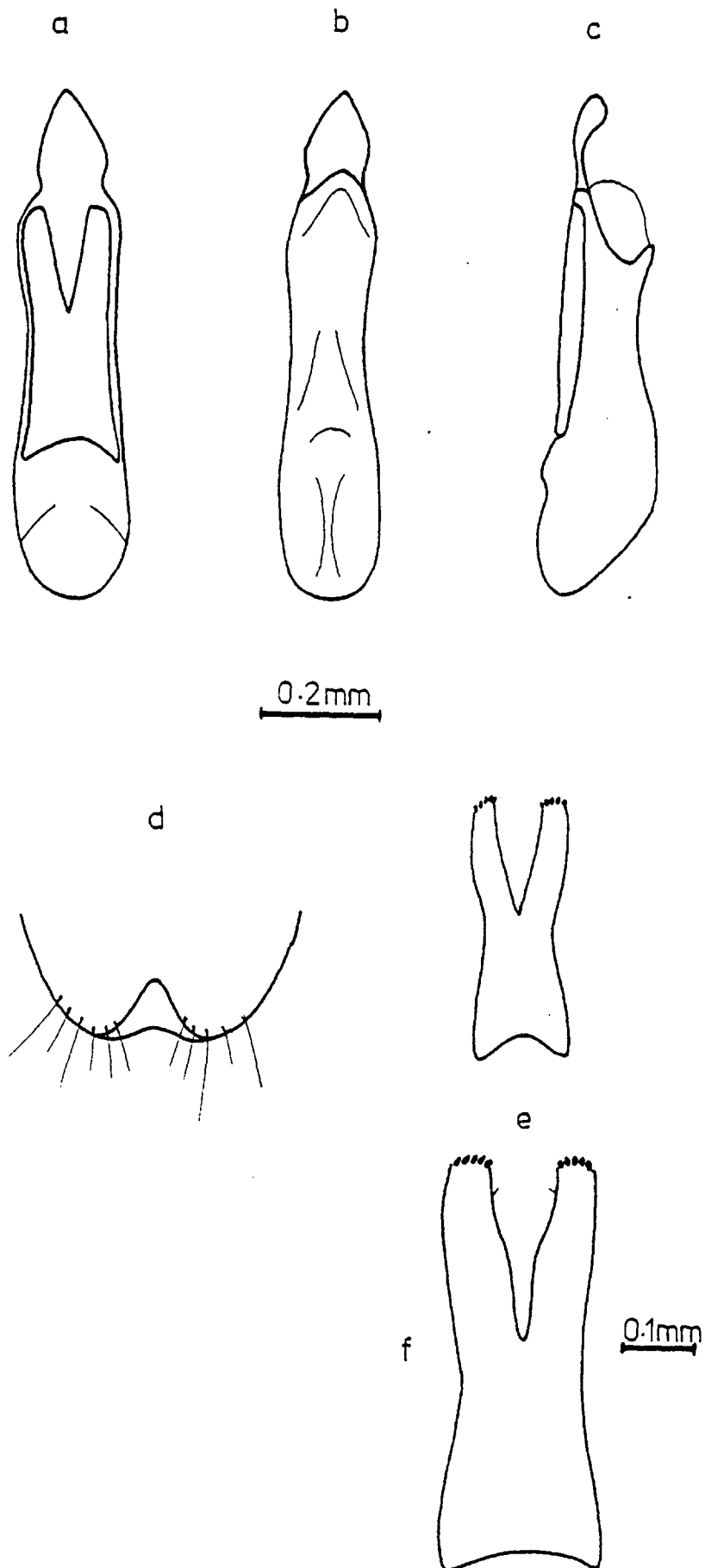
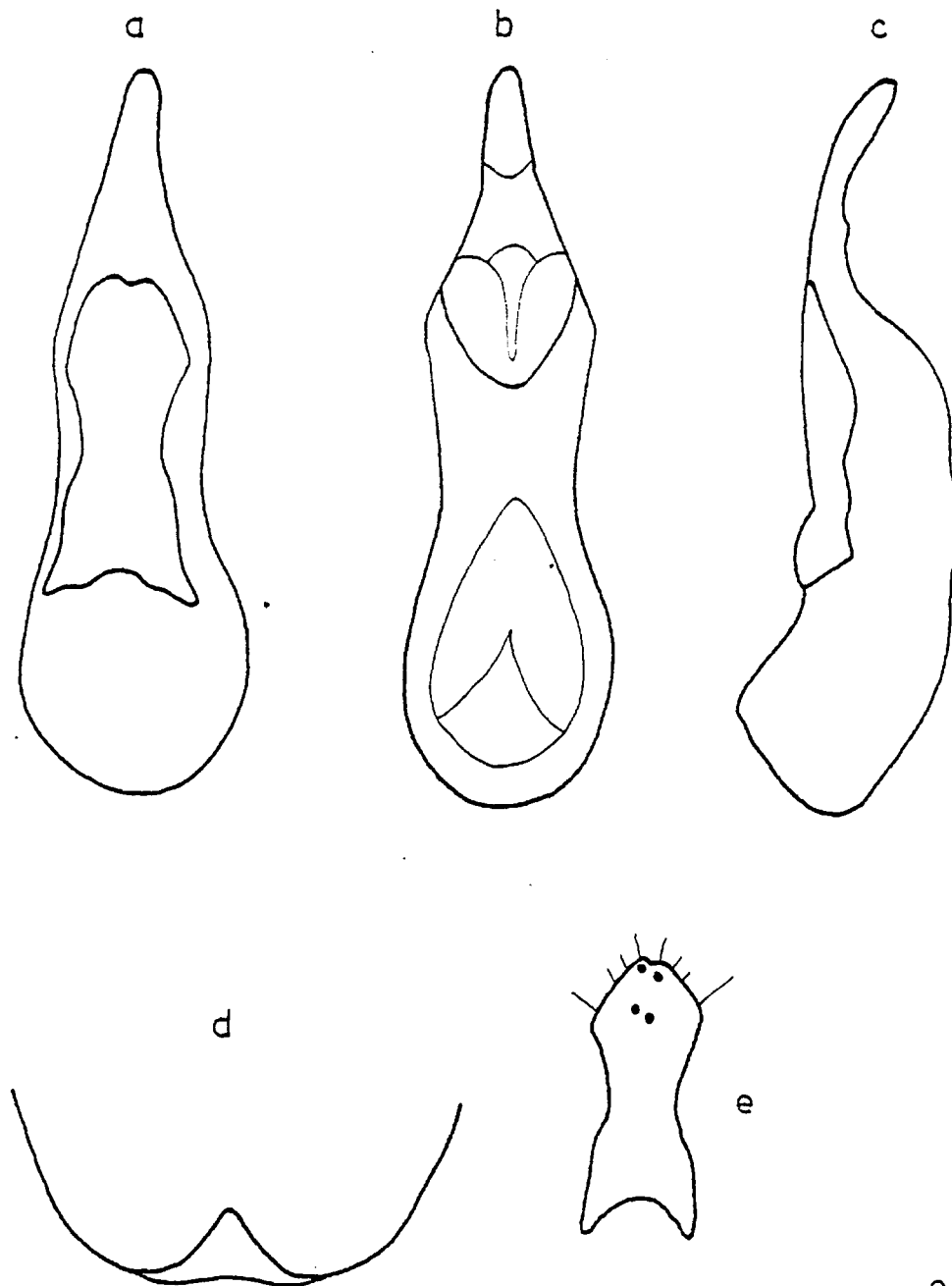


Fig.4.48 Male genitalia of Gabrius trossulus; a) median lobe ventral view, b) median lobe dorsal view, c) median lobe lateral view, d) sternite VIII, e) lateral lobe.



Gabrius hesperius Group

In this north African group of species the males have remarkable secondary sexual characters (Coiffait, 1964). There are five species in the group; 4 were previously described under the name G. hesperius and 2 under G. dentipes.

G. cobosi Coiffait Andalusia.

G. dentipes (Eppelsheim) Aragon, Moroccan mountains.

G. hesperius Fauvel Algeria and Tunisia.

G. normandi Smetana Algeria and Maroc (Portugal).

G. peyerimhoffi Coiffait. Algeria.

The females of the group are very difficult to distinguish, but male determination is easy using the secondary sexual characters.

Secondary Sexual Characters

The ♂ genitalia are figured, (Figs. 4.49-4.50, after Coiffait, 1964).

G. cobosi

hind tibia: distinctly flattened in the vertical plane, terminating at the internal edge in a small tooth which bears a large spine. Internal border with dense setae.

G. dentipes

hind femur: large triangular rooth at the posterior border behind the apex.

hind tibia: sinuated in middle. At centre apex a dense fringe of long pliant setae.

G. hesperius

hind tibia: feebly curved, slightly flattened in the vertical plane, internal face with long dense setae.

G. normandi

hind tibia: distinctly flattened in the vertical plane, feebly curved, devoid of apical broadening, internal edge with dense long setae.

Fig.4.49 Male genitalia of Gabrius; i. median lobe lateral view, ii. median lobe ventral view, iii. lateral lobe, a) G.dentipes, b) G.peyerimhoffi, c) G.hesperus.

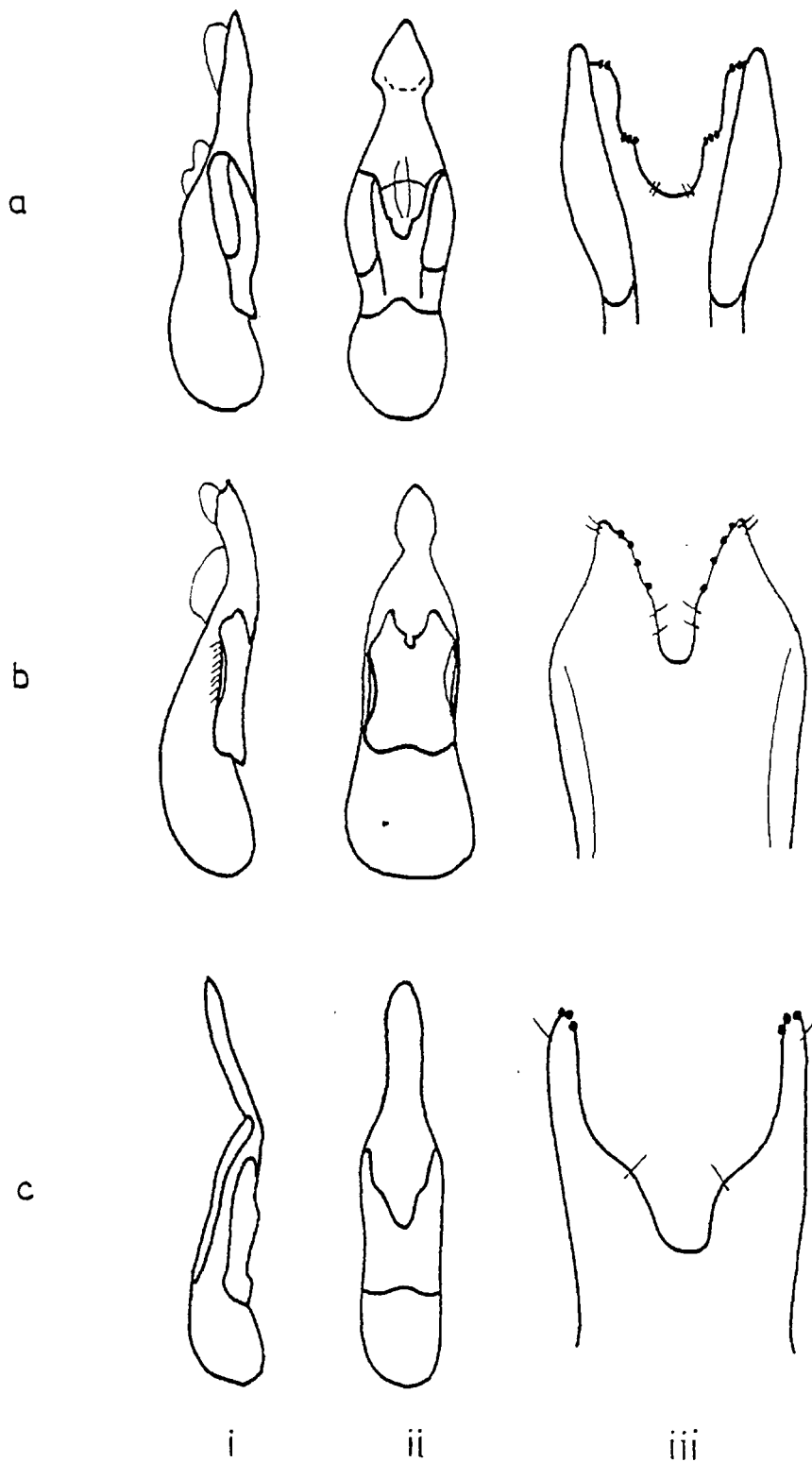
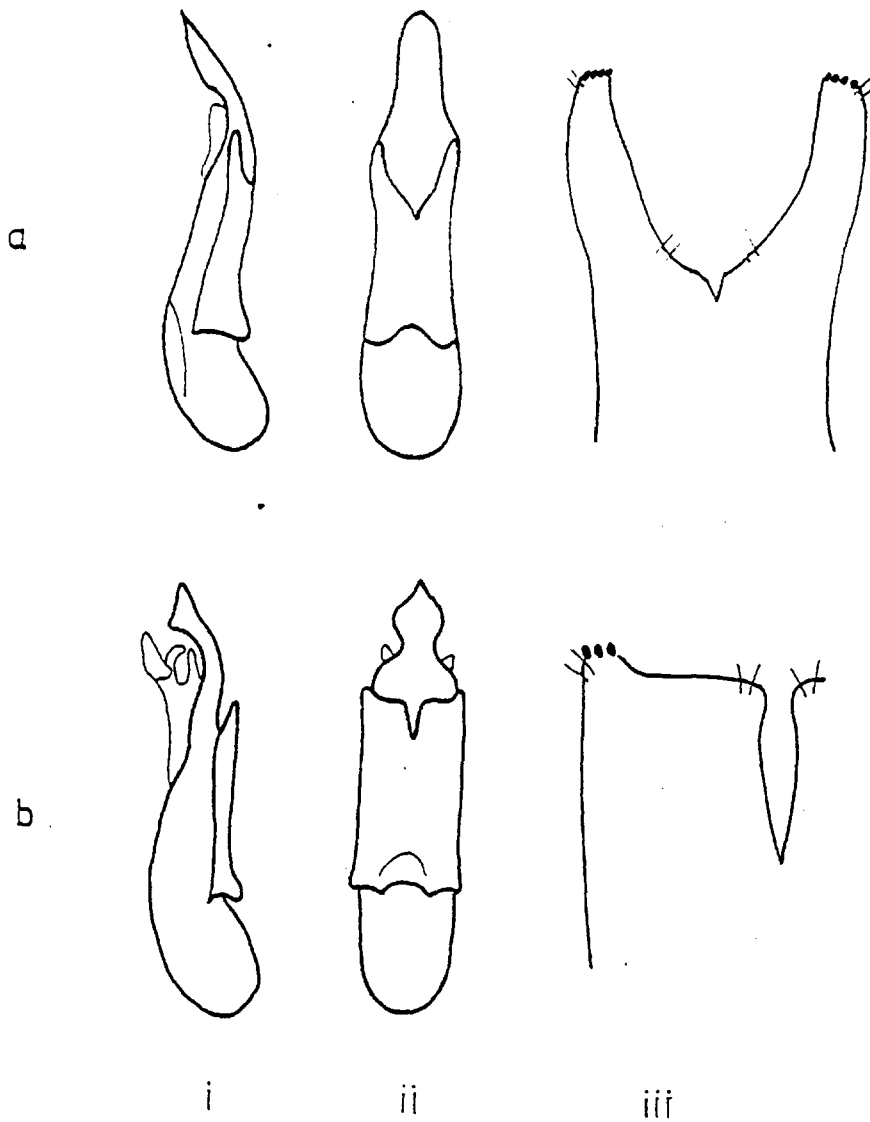


Fig.4.50 Male genitalia of Gabrius; i. median lobe lateral view,
 ii. median lobe ventral view, iii. lateral lobe,
 a) G.normandi, b) G.cobosi.



G. peyerimhoffi

hind femur and tibia: simple, but covered on posterior half of internal face with fringe of more or less long setae.

Function

The members of the G. hesperius group are mostly sympatric. The positioning of the peg setae emphasise the difference in shape of the lateral lobe. This may be used as part of a tactile signalling system.

Staphylinus LinnaeusS. globulifer FourcroyS. melanarius HeerS. winkleri BernhauerDistribution and Habitat

Detailed distribution is given by Horion (1965) and Chapman (1934).

S. globulifer

West, south and central Europe, and southern north Europe;

Asia Minor, north to Denmark and southern Sweden.

S. melanarius

North and central Europe; Caucasus; southern European

distribution not well established.

S. winkleri

South and central Europe; southern north Europe.

S. winkleri is more numerous in southern Europe than S. melanarius. S. globulifer is the most infrequent of the S. melanarius group, its dispersal being isolated. However, the three species are broadly sympatric in England, northern France, Belgium, Holland, West Germany, Switzerland, eastern Austria, Balkans, Czechoslovakia and southern Sweden. Records in the BMNH and Steel (1948) indicate that all three species are widely distributed and fairly common in the south of Britain but rare further north.

All three species share a similar type of habitat in dry, open country, meadows and fields, but also in moist places, under stones, moss and rotting vegetation. All three species have been found syntopically.

Secondary Sexual Characters (Coiffait, 1956)

Only very recently have the three species been separated, they were all previously known under the name S. morio Grav., owing to difficulty in differentiating them (Steel, 1948). The secondary sexual characters of the males enable the species to be distinguished.

The fourth segments of the male maxillary palpi are distinctly stouter than those of the female, and the third segments of the labial palpi are moderately widened internally in males. The posterior margin of the eighth sternite is shallowly, triangularly emarginate in the male and simple in the female.

S. globulifer (Fig. 4.51& 4.52)

Median lobe: the apex is asymmetrical and the side facing the lateral lobe with a black, heavily chitinated and heavily sculptured part of the internal sac.

Lateral lobe: asymmetrical and apically indented; the distal half is heavily chitinated and strongly sculptured, the proximal half is less strongly chitinated.

S. melanarius (Fig. 4.53)

Median lobe: with asymmetrical apex.

Lateral lobe: asymmetrical inclined laterally in the apical half. Truncated at the apex. Inside face spoon shaped with a row of short spicules on each side, and outer edges with short setae.

Internal sac: with armature.

S. winkleri (Fig. 4.54& 4.55)

Median lobe: with asymmetrical apex.

Lateral lobe: asymmetrical, with slight lateral inclination at the extreme apex. Inside face spoon shaped with a row of short spicules near to outside edges.

Internal sac: with armature.

Variation

There is overall size variation in the genitalia. S. globulifer exhibits minor variation in the shape of the apex of the lateral lobe where the lateral inclination is sometimes more abrupt.

S. winkleri and S. melanarius exhibit variation in the numbers of spicules on the lateral lobe.

Fig.4.51 Male genitalia of Staphylinus globulifer; a) ventral view, b) dorsal view, c) lateral view.

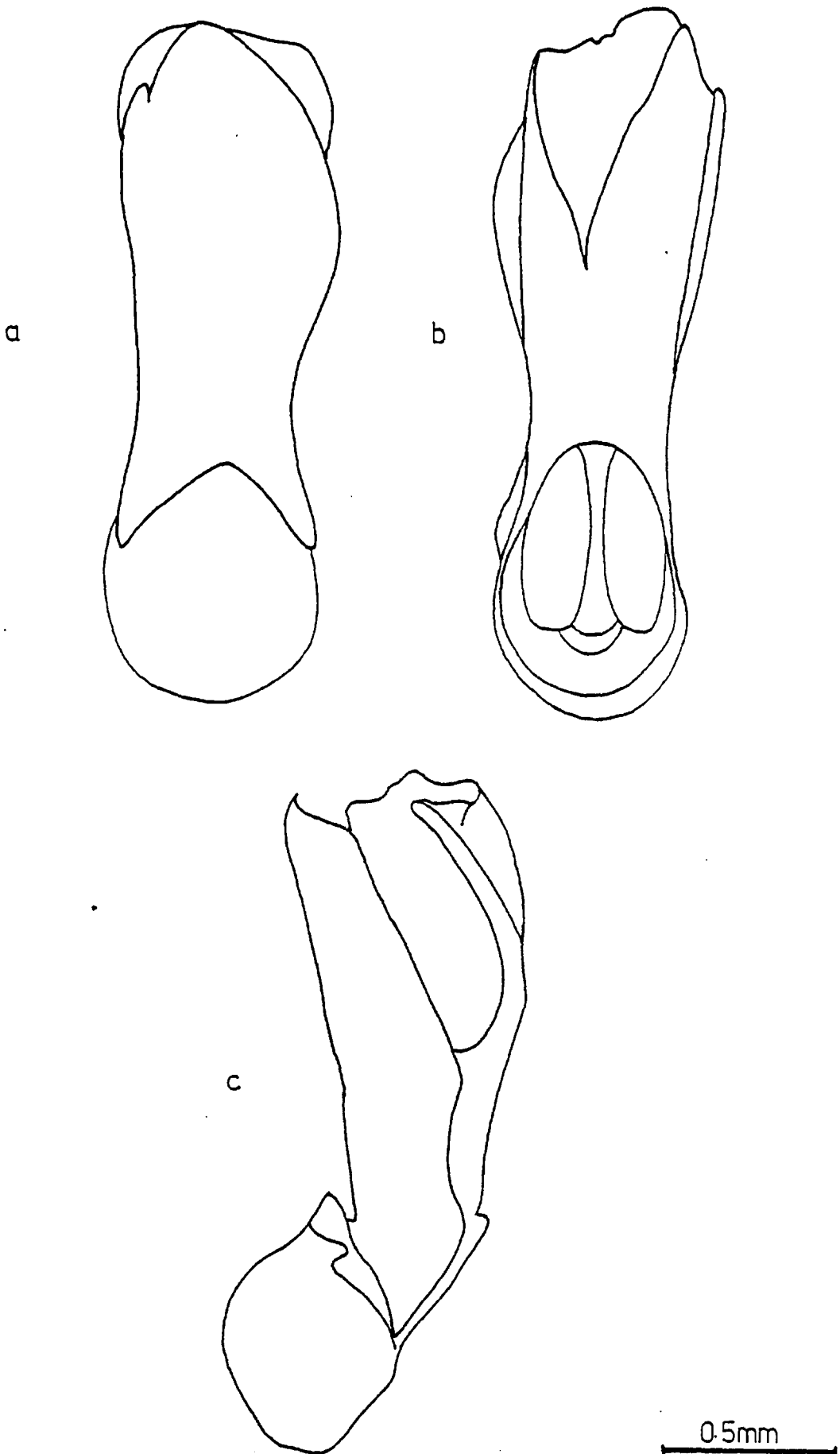
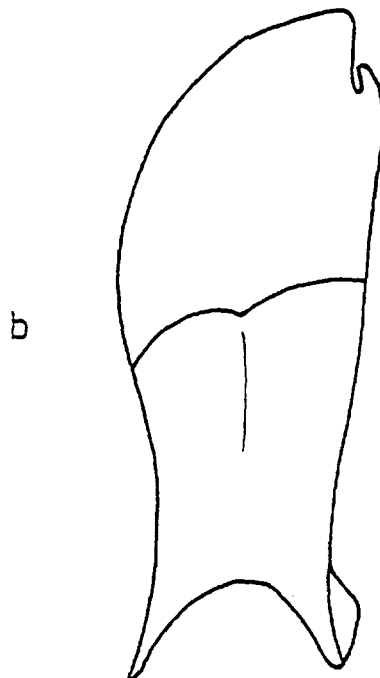
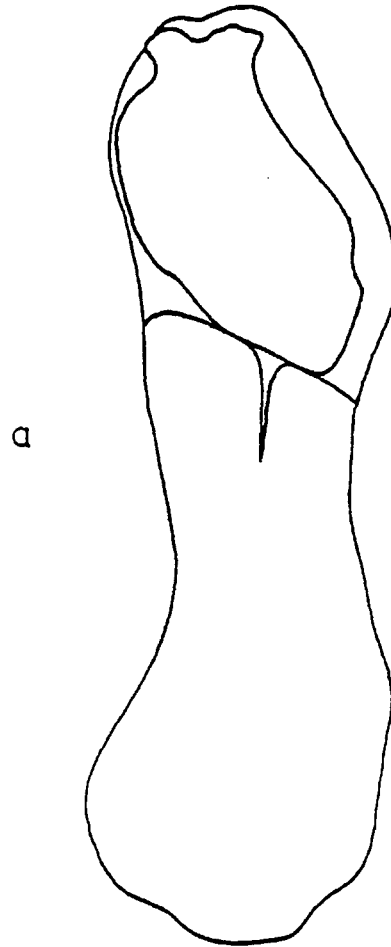


Fig.4.52 Male genitalia of Staphylinus globulifer; a) ventral view with lateral lobe removed, b) dorsal surface of lateral lobe.



0.5mm

Fig.4.53 Male genitalia of Staphylinus melanarius; a) ventral view, b) lateral view, c) dorsal view, d) dorsal view of lateral lobe, e) ventral view with lateral lobe removed.

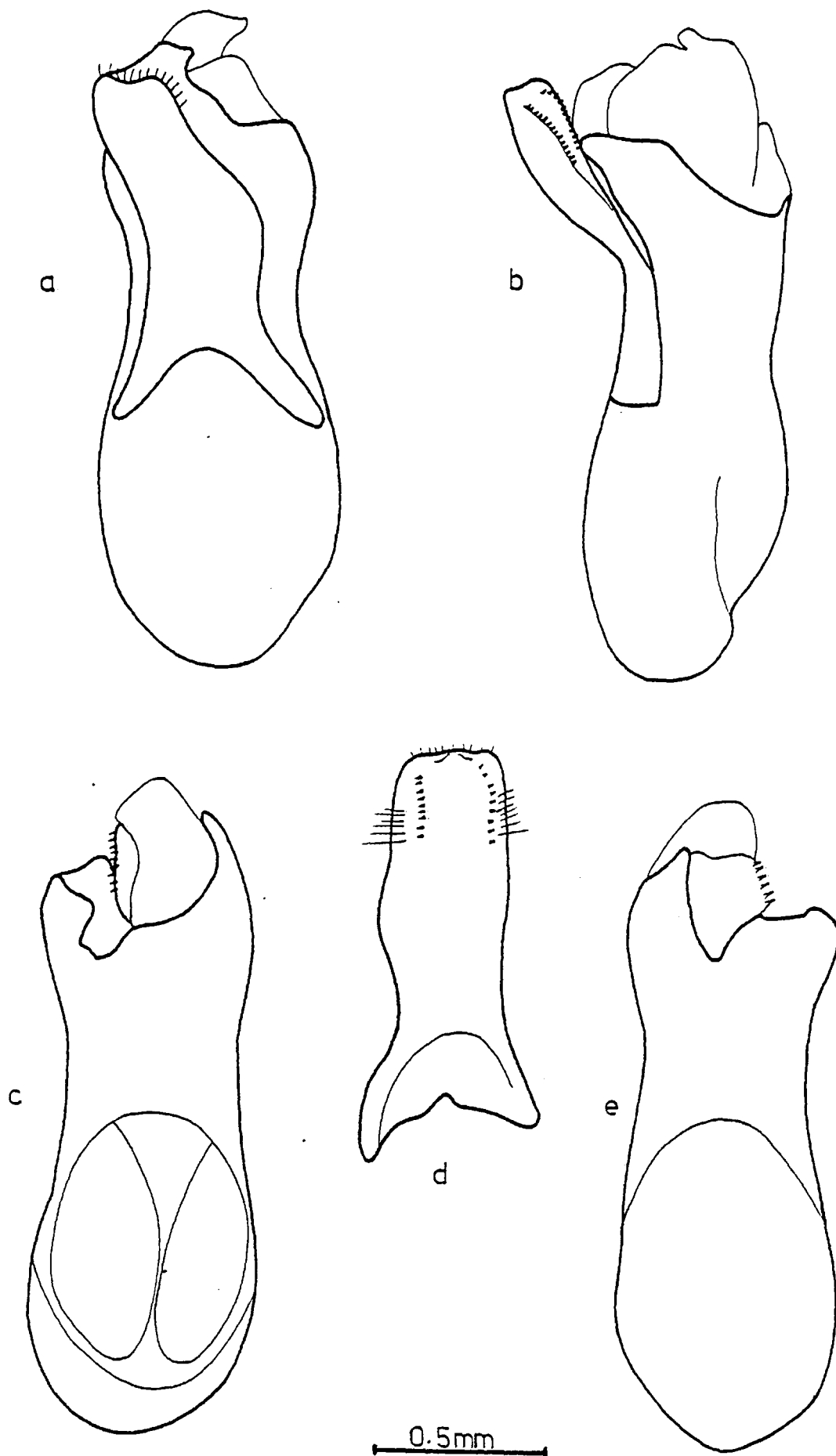


Fig.4.54 Male genitalia of Staphylinus winkleri; a) ventral view, b) lateral view, c) dorsal view of lateral lobe.

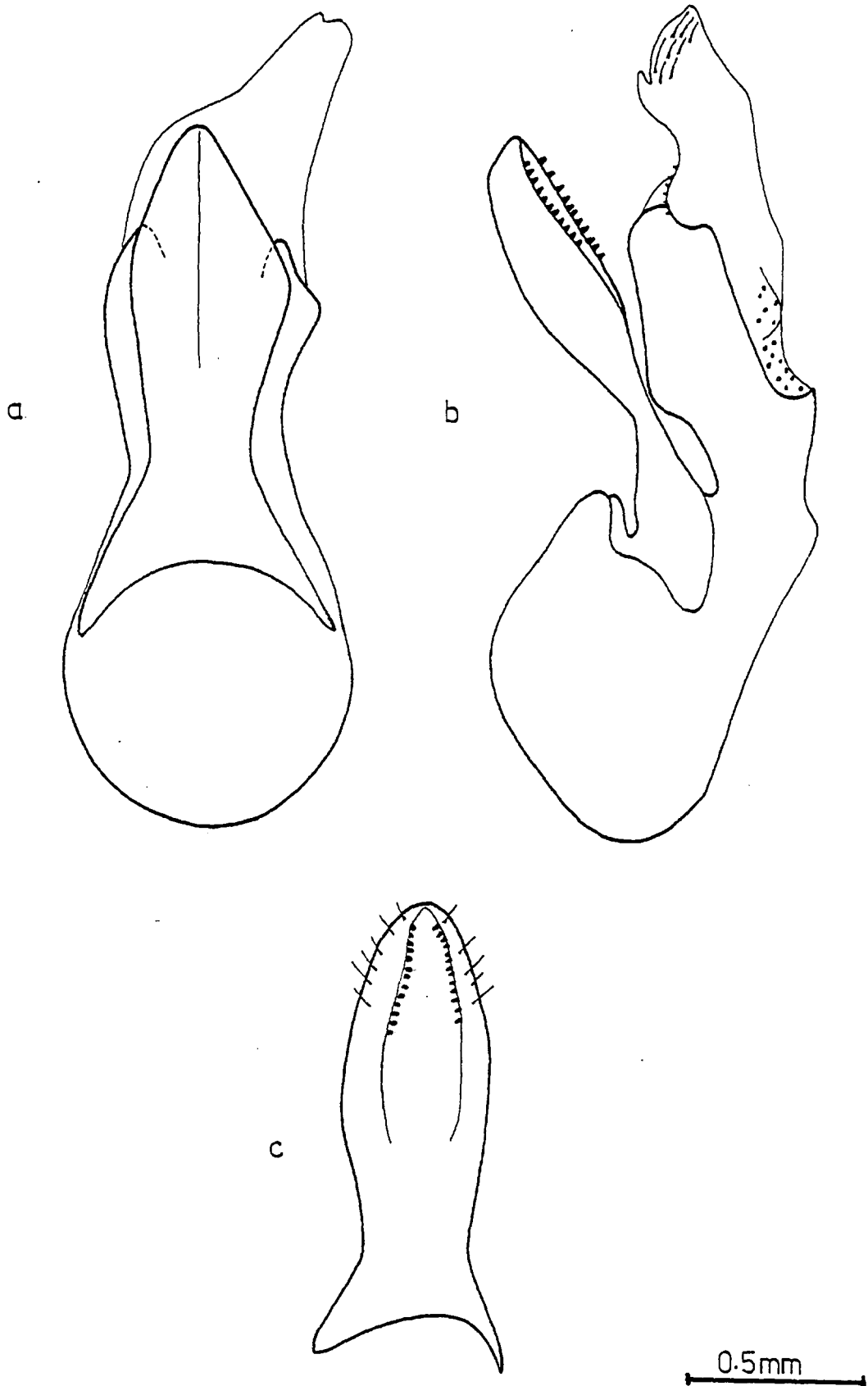
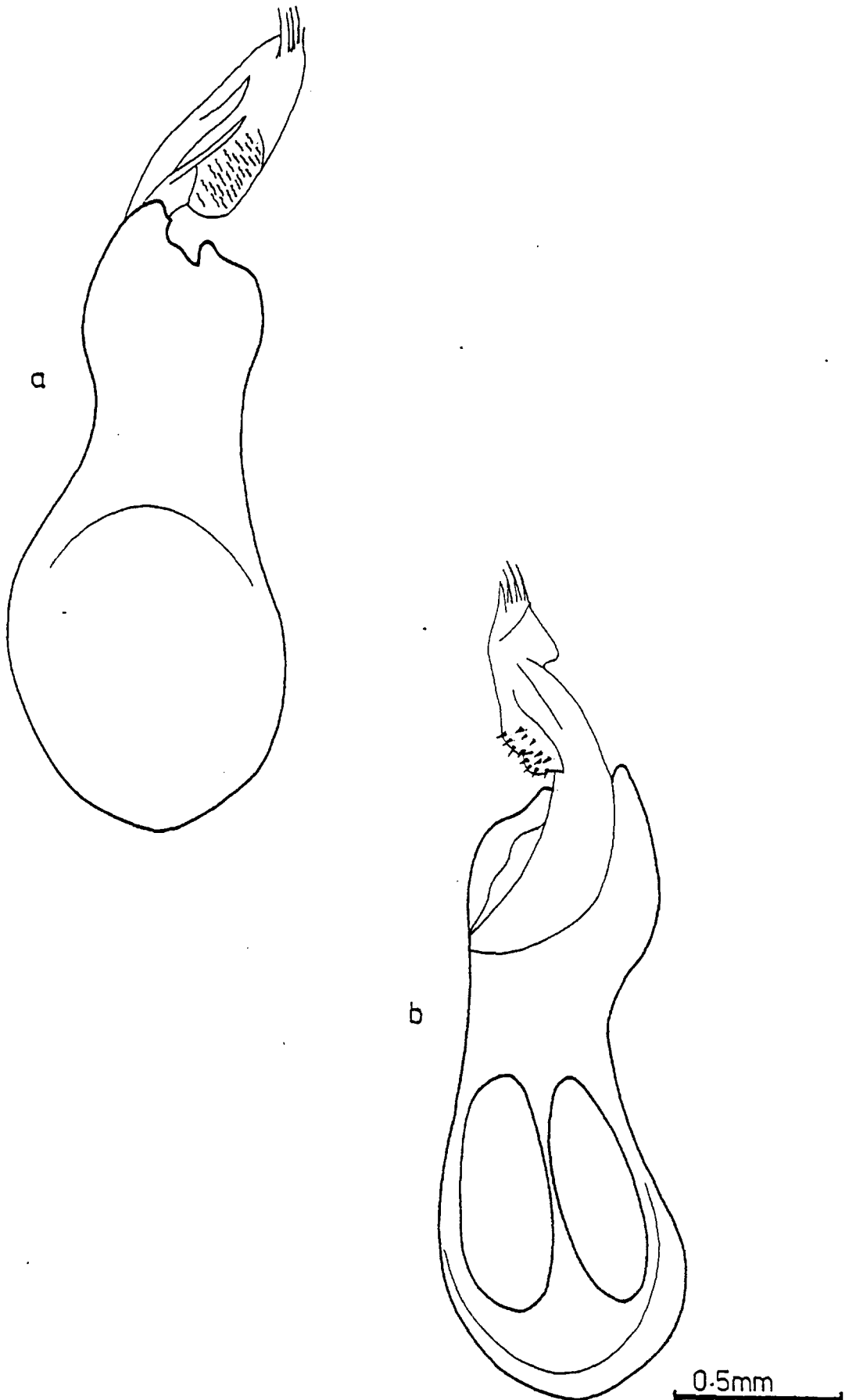


Fig.4.55 Male genitalia of Staphylinus winkleri; a) ventral view with lateral lobe removed, b) dorsal view.



Quedius StephensRange of Variation with the Genus

Quedius species exhibit the same types of differences in the secondary sexual characters as Philonthus, although the extremes of variation are probably less marked.

Some North American examples documented and figured by Smetana (1971) are used to illustrate this.

1. Quedius pellax Smet. and Q. limbifer Horn

The pair are extremely similar in all external characters; however, the differences in the secondary sexual characters of the genitalia are distinct and constant. Both species share the same geographical range: western North America, from southern California to southern British Columbia. Although information is limited their habitats seem to be the same, occurring in various debris, floor litter and fallen leaves mainly in forested areas.

2. Quedius narada Hatch, Q. paradisi Hatch and Q. frater Smet.

These species form part of a homogeneous group which are very similar to one another in external characters. Secondary sexual male characters are present on the seventh and eighth sternites and on the genitalia.

Q. narada and Q. paradisi are likely to be sympatric, and probably also Q. frater with Q. paradisi in mountainous areas of Washington and Oregon. Q. frater is only known from the Olympic Mountains. The habitats are not well known but the species have been found in various debris, particularly in wet areas.

3. Quedius breviceps (Csy.) and Q. densiventris (Csy.)

Both species are very similar and can only be distinguished on genitalic characters. Q. densiventris is transcontinental from Alaska to Newfoundland and Colorado to New York. Q. breviceps is a western species occurring from California to Alaska. Both are sympatric

and are found in set biotopes of various debris, including moss and fallen leaves.

Examples from species occurring in Britain are:

Q. curtipennis Bernhauer

Q. fuliginosus (Gravenhorst)

Distribution and Habitat

Detailed distribution is given by Horian (1965).

Q. curtipennis

Europe, Asia Minor.

Q. fuliginosus

Palearctic species: Europe (Mediterranean to extreme north), north Africa, Asia Minor, Caucasus, Siberia and north China.

Both species are widely distributed throughout Britain, both occurring syntopically in woods and also in open damp places, under moss, leaves, various rotting debris, under bark and under stones.

Frank (1968) suggests there may be a difference in breeding times between the two species, from May to June in Q. fuliginosus and from October to January in Q. curtipennis.

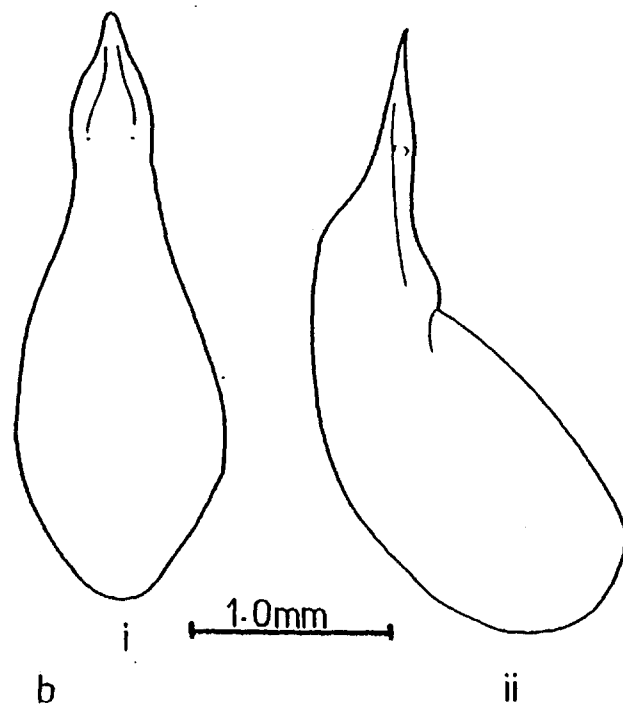
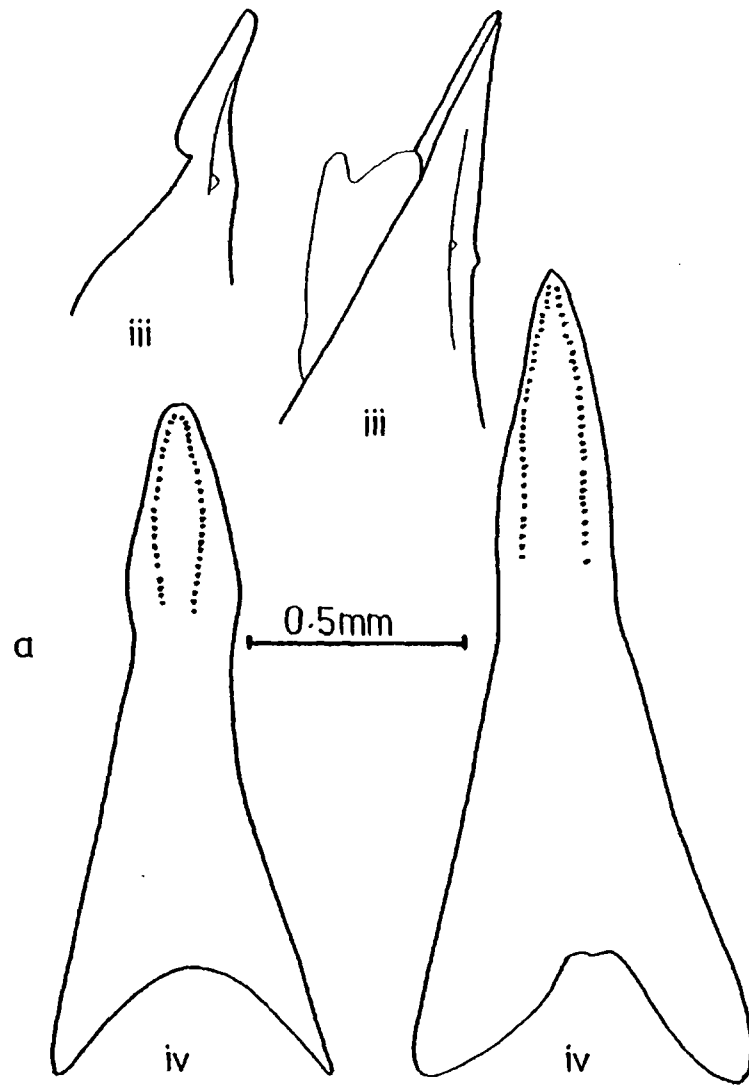
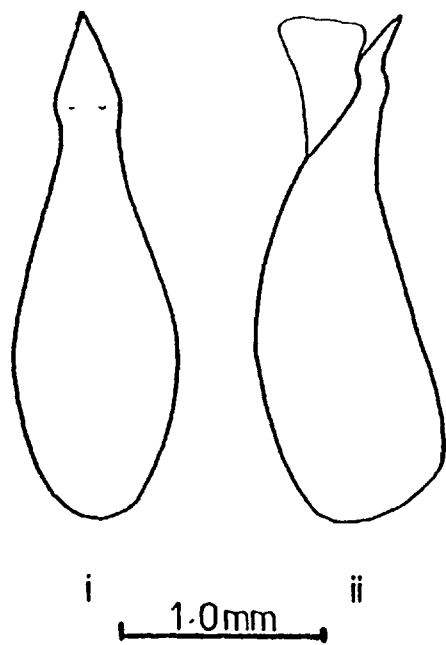
Secondary Sexual Characters

Q. fuliginosus and Q. curtipennis are extremely similar with only minor external differences, the females being particularly difficult to distinguish. At first appearance the ♂ genitalia look extremely similar; however, there are distinct differences which are constant. The differences are perhaps not so striking as might be expected in two such closely related syntopic species. The secondary sexual characters are of the typical staphylinine type, the distinctive differences being: Q. fuliginosus (Fig. 4.56a)

The length of the median lobe and lateral lobe is shorter than those of Q. curtipennis.

Median lobe: the apex when viewed laterally is broadened with distinct indentation near the foramen.

Fig.4.56 Male genitalia of Quedius; i. median lobe ventral view,
ii. median lobe lateral view, iii. median lobe apex,
iv. lateral lobe, a) Q.fuliginosus, b) Q.curtipennis.



Lateral lobe: broadens before tapering to the rounded apex, with a peg pattern quite distinct from Q. curtipennis. There are two curved columns converging at the anterior and posterior extremities of the lateral lobe.

Q. curtipennis (Fig. 4.56b)

The median and lateral lobes are longer than those of Q. fuliginosus.

Median lobe: when viewed laterally the apex is tapered.

Lateral lobe: tapers to apex, with a larger peg pattern of two straight columns of peg setae situated towards the outer edges and converging at anterior extremity only.

Quedius mesomelinus (Marsham)

Quedius maurus (Sahlberg)

Distribution and Habitat

The European distribution of the two species is detailed in Section 6. British distributions are shown in Maps 6 and 7.

Further details are given by Horion (1965).

Q. mesomelinus

Almost cosmopolitan. Palaearctic region, Iceland, Greenland, North and South America, Australia and New Zealand.

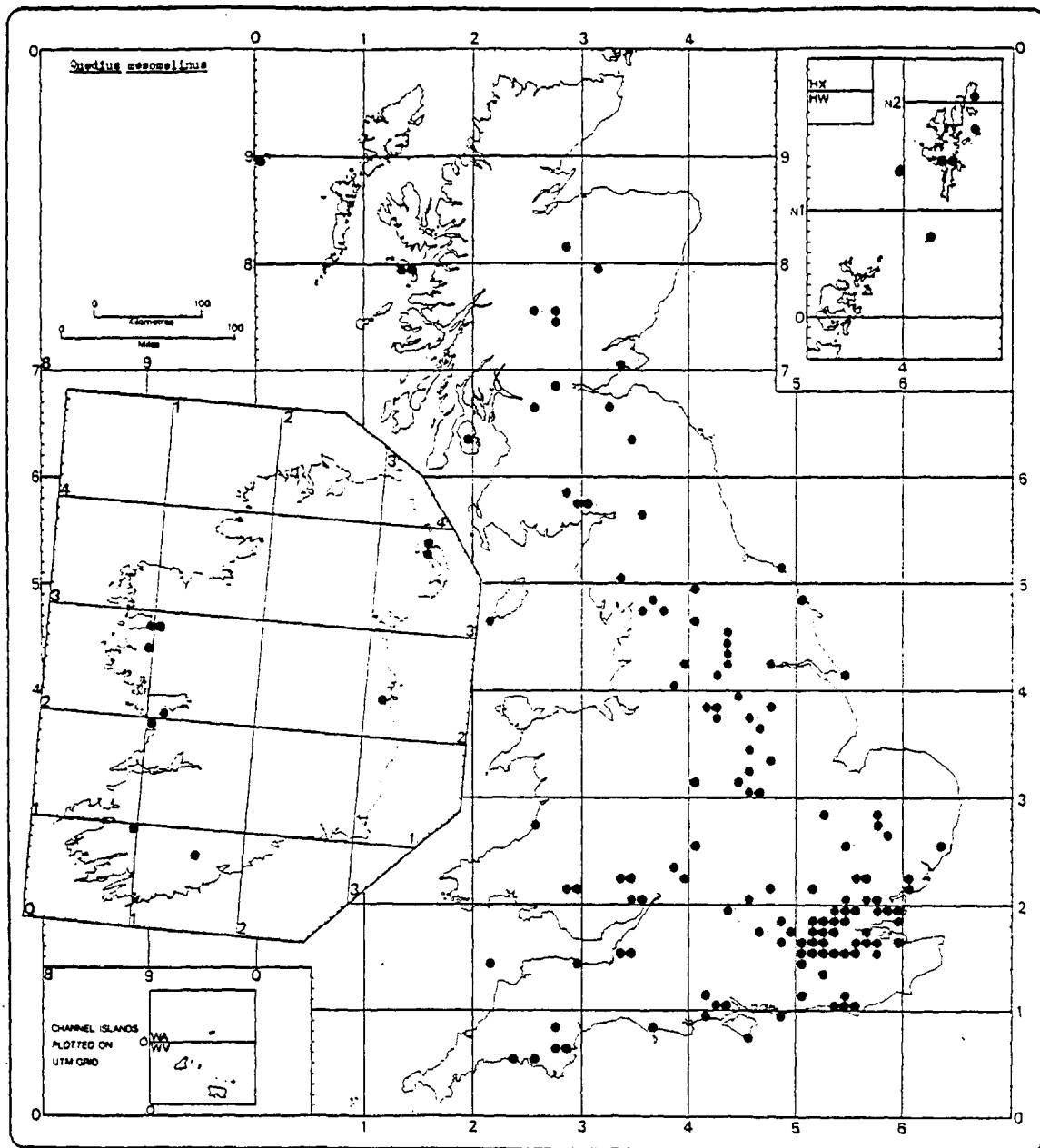
Q. maurus

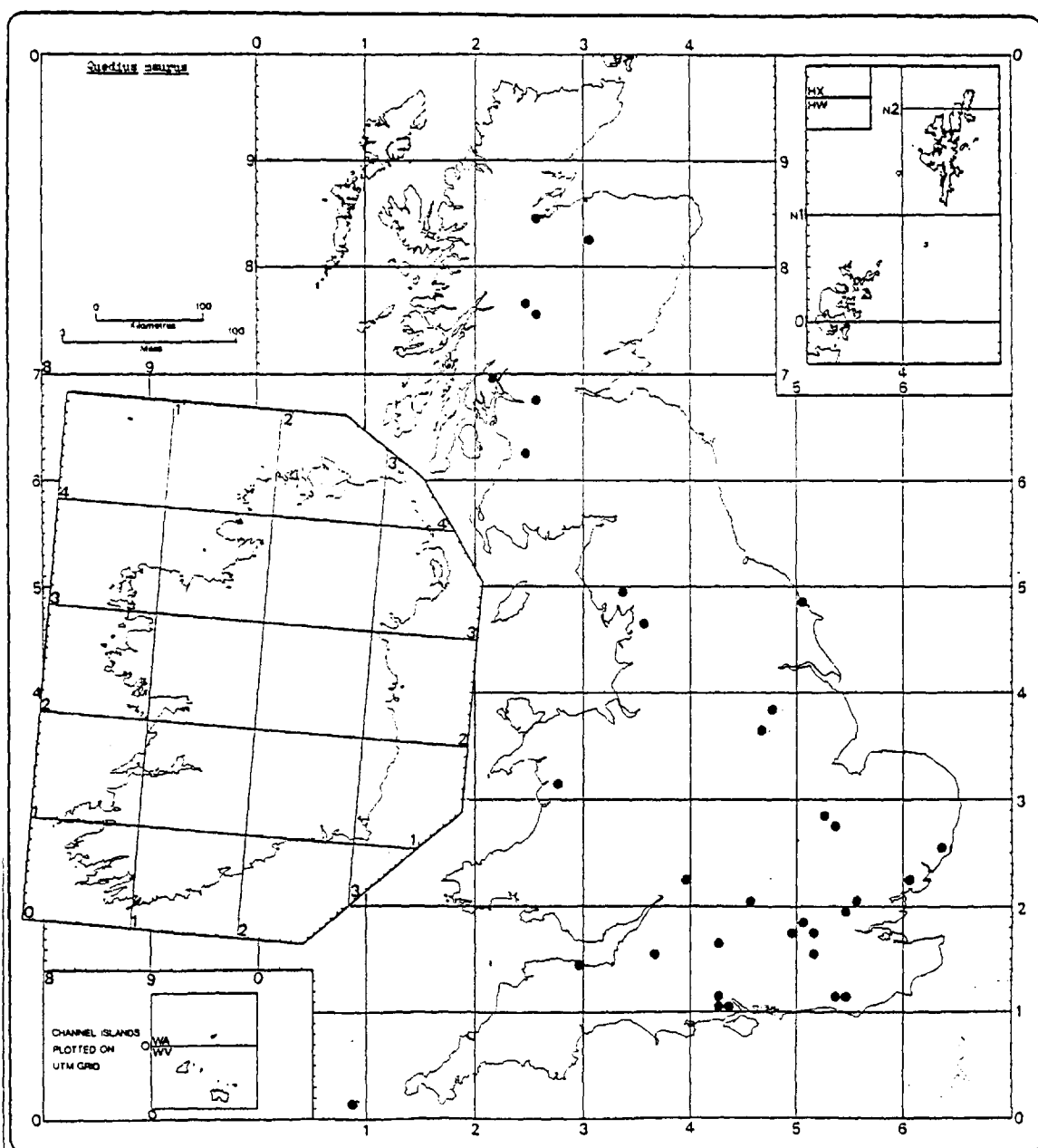
North and central Europe and Caucasus.

Both species are widely distributed in Britain. Q. mesomelinus is common in rotting vegetation, compost heaps, moss, leaves, fungi, and at the entrances of caves and in animal burrows. Q. maurus has a more restricted, or local, distribution and is found in the same habitats as Q. mesomelinus but more frequently occurs under bark.

Secondary Sexual Characters

The two species are indistinguishable using external characters alone, except that Q. maurus is generally the smaller of the two.

Map 6. Distrubution of Quedius mesomelinus in the British Isles.



Females are difficult to determine, but the males are easily distinguished using the secondary sexual characters of the genitalia.

The male eighth sternite is triangularly emarginated.

Q. mesomelinus (Fig. 6.2)

Median lobe: apex with a wide central ridge and two widely spaced projections on either side of the lobe just posterior to the ridge.

Lateral lobe: the apex is indented in the mid-line with a specific peg pattern.

Q. maurus (Fig. 6.3a-c)

Median lobe: the apex has a narrow central ridge.

Lateral lobe: this is narrow in comparison with Q. mesomelinus and has a distinct specific peg pattern.

Variation

Intra-specific geographical variation is treated in detail for these two species, and the European subspecies of Q. mesomelinus in Section 6.

Function

Mating behaviour is described in Q. mesomelinus and Q. tristis (Section 5.2.8 and 5.2.9), in relation to the function of the secondary sexual features.

Amblyopinina (Seevers 1955)

The Amblyopinina are obligate ectoparasites on rodents and marsupials. The group is morphologically linked to the tribe Quediini, some genera being doubtfully separable on structural grounds. The group occurs exclusively in the subtropical and temperate zones of the Neotropical region.

There is a high degree of host-specificity. They are flightless and remain closely associated with the host at all times, feeding either on blood, body fluids or epidermal secretions, or encrustaceans.

As most species are host-specific and therefore allopatric, it is interesting that characters of the genitalia exhibit what could be recognition differences between species. Figures are given by Seevers (1955).

Amblyopinus

1. The apex of the lateral lobe differs in shape between species. The size and distance between the four setae on each side and the peg pattern are specific.
2. The numbers of long setae on the eighth sternite of the male are different in separate species.

Amblyopinodes

1. The apex of median lobe is specific.
2. There are minor differences in the apex of the lateral lobe.
3. The internal sac armature exhibits differences between species.
4. Some lateral lobes bear peg setae, while some do not. Where pegs are present, the pattern differs between species.
5. The males possess claviform setae on sternites III - IV.

Megamblyopinus

1. There are differences in the peg pattern and numbers of setae on the lateral lobe in different species.

Edrabus

1. The apex of the lateral lobe exhibits differences between species.
2. The position of setae on lateral lobe are specific.
3. There are differences in peg pattern and in the length of pegs.
4. The internal sac armature may be specific.

Some differences between species are more pronounced than others. However, it is difficult to postulate a function for features which are of a type likely to be used in recognition but where species do not occur sympatrically.

4.366 Tachyporinae.

The Tachyporinae are a disparate group and will be considered under the two tribes Bolitobiini and Tachyporini.

Bolitobiini

The Bolitobiini occur in litter, moss and fungi but there are none in putrifying habitats. In general male secondary sexual characters afford poor differences between species. However, in the few examples which do exhibit good differences, closely related species are found together.

Mycetoperus Mannerheim

M. longicornis "Maklin

M. splendidus (Gravenhorst)

Distribution and Habitat

Details are given by Horion (1967).

M. longicornis and M. splendidus are sympatric throughout much of their distribution.

M. longicornis

Palearctic; in Europe from extreme north to the Mediterranean area and north Africa; Asia Minor, Caucasus, Transcaucasus, Turkey and east Siberia.

M. splendidus

Palearctic and North America.

The British distribution of the two species, based on specimens in the BMNH, is similar. Both species can be found in similar

habitats, including moss (wet sphagnum on moors), rotting leaves, moist, boggy or marshy places, pools, ditches and nests. In addition, M. splendidus is reported from dry sandy soils in pine forests and in litter formed from dead needles.

Secondary Sexual Characters

In the males the sternites of the sixth, seventh and eighth abdominal segments have their posterior margins modified, with dense brushes of setae. The males of the two species are distinct in this respect, while the females have no corresponding differences (Fig. 4.57-4.58).

The apical structure of the aedeagus differs slightly in the species, but is probably only a comparative difference (Fig. 4.59).

Bolitobius Samouelle

B. analis (Fabricius)

B. cingulatus (Mannerheim)

Distribution and Habitat

Details are given by Horion (1967).

B. analis

Europe, Caucasus, and north America.

B. cingulatus

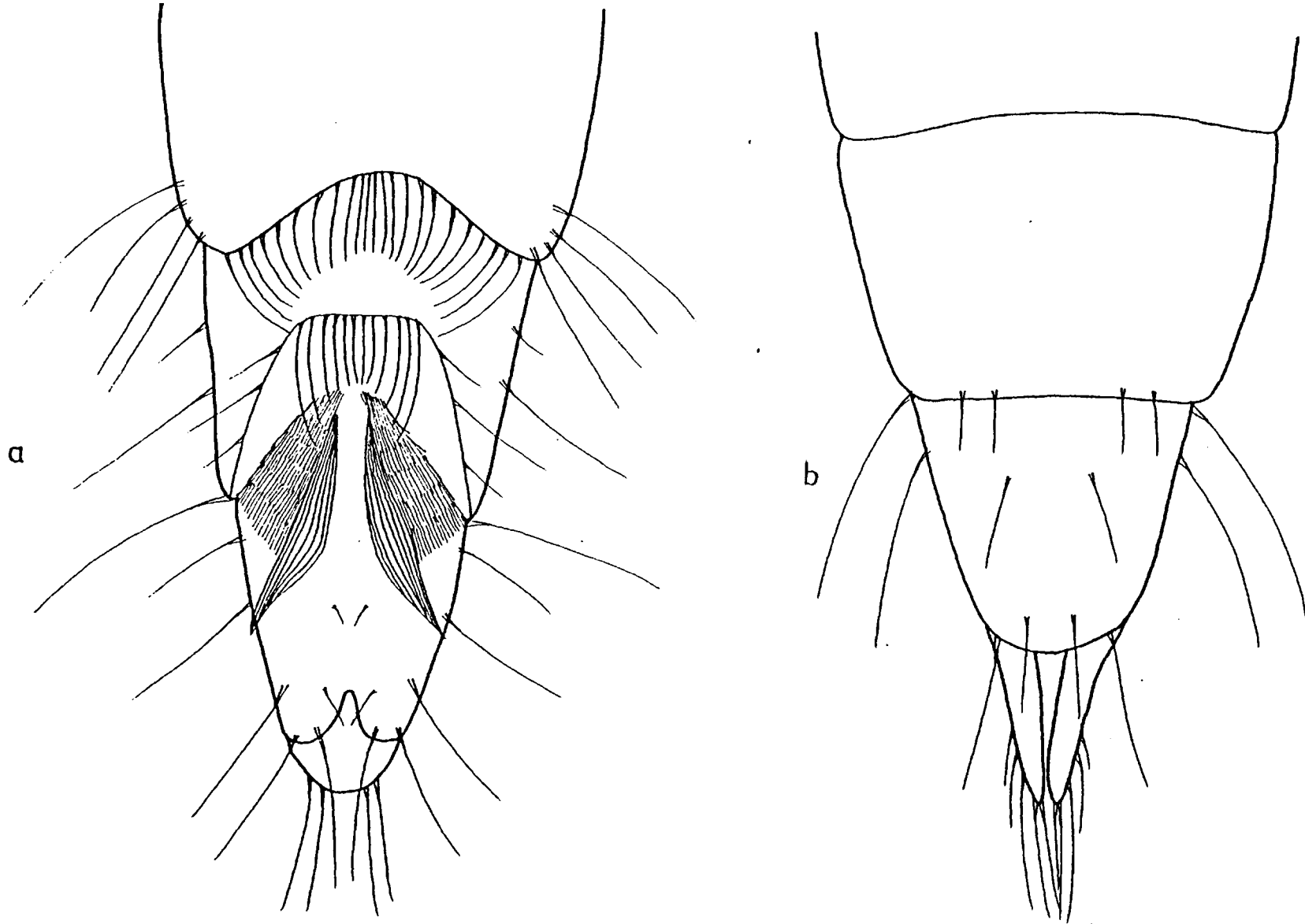
Palaearctic and north America.

The British distribution of the two species is similar, being common and widespread. The species occur in dry and moist biotopes including moss, rotting leaves, rotting fungi, rotting wood, pine needles, nests and under Calluna.

Secondary Sexual Characters

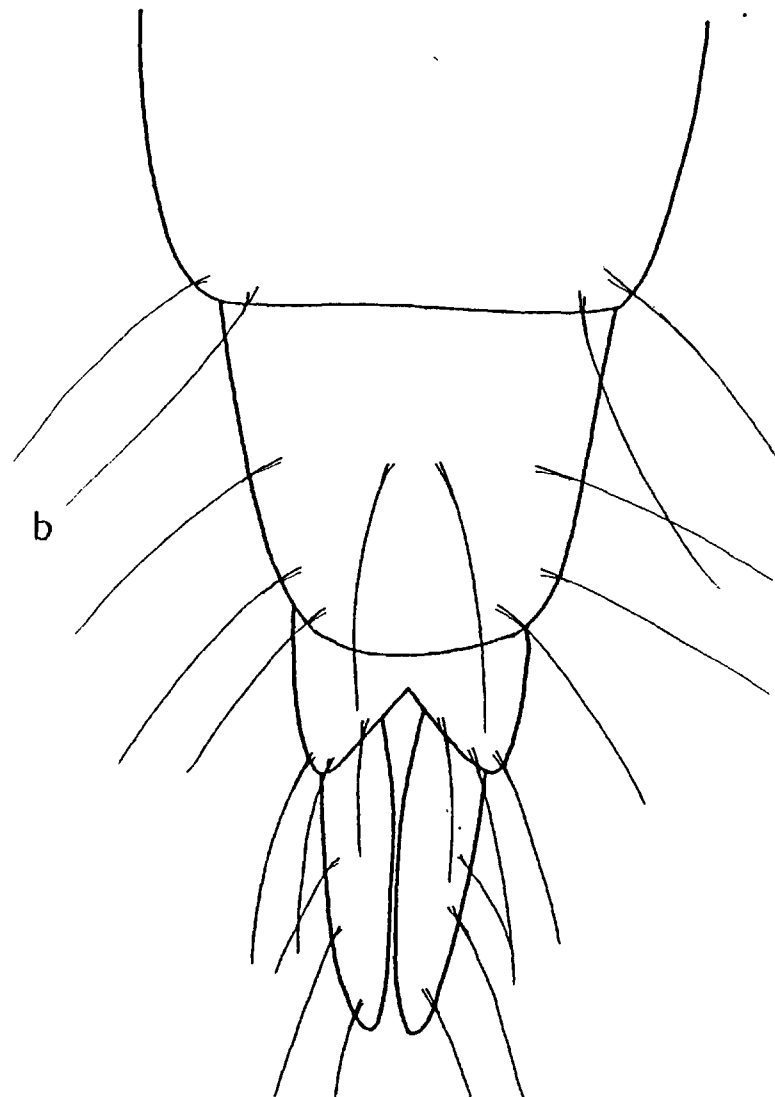
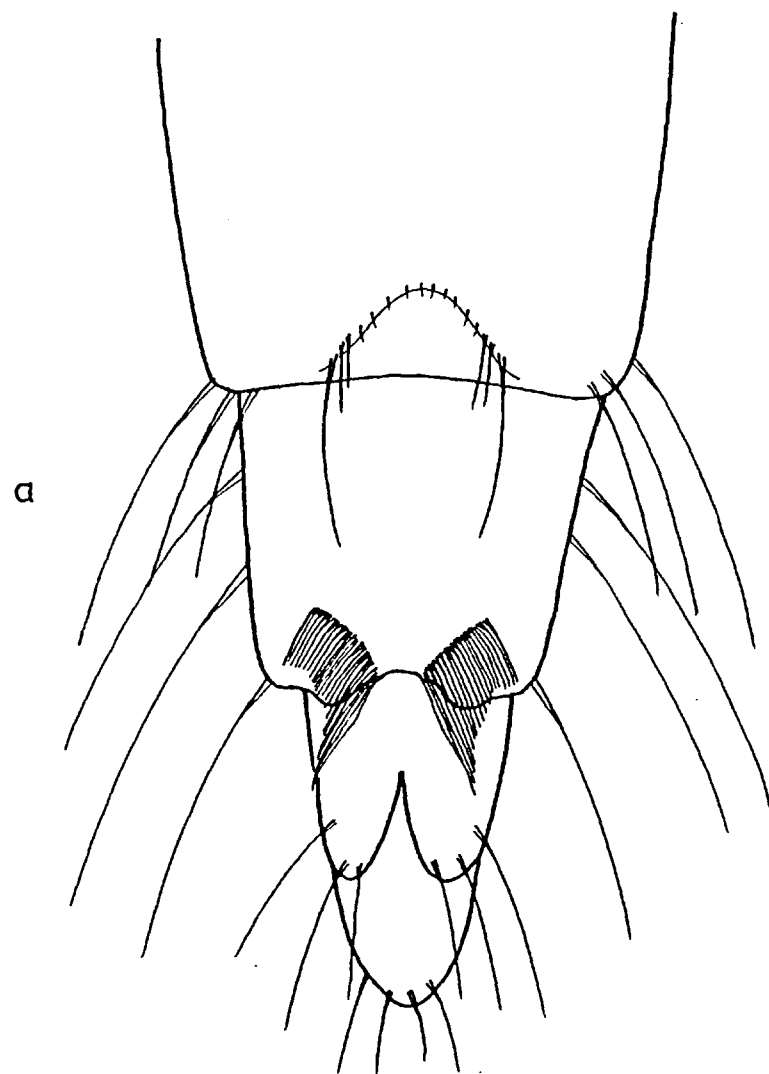
The same types of differences are present as in Mycetoporus, but they are not so striking.

Fig.4.57 Abdomen of Mycetoporus splendidus; a) ventral view male, b) ventral view female.



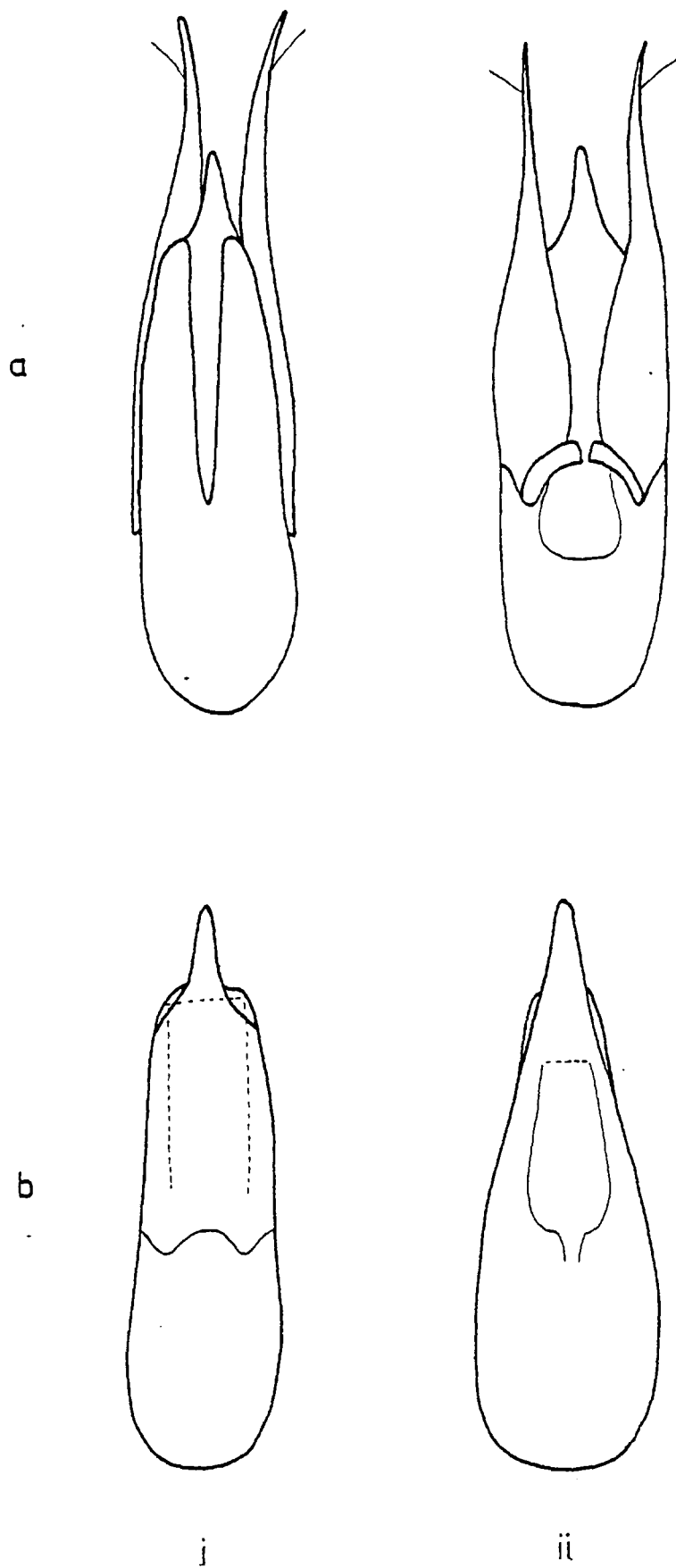
0.2mm

Fig.4.58 Abdomen of Mycetoporus longicornis; a) ventral view male, b) ventral view female.



0.2mm

Fig.4.59 Male genitalia of Mycetoporus; i. dorsal view, ii.ventral view, a) M.longicornis, b) M.splendidus.



B. analis (Fig. 4.60 a & b, 4.61 a)

Sternite VIII : posterior margin produced into a central lobe, with a dense brush of setae leading from the lobe anteriorly in the mid-line.

Aedeagus : apically distinct.

B. cingulatus (Fig. 4.60 c & d, 4.61 b)

Sternite VIII : posterior margin produced into an apically drawn out lobe, with a dense brush of setae leading from the lobe anteriorly in the mid-line.

Aedeagus : apically distinct.

Tachyporini

Tachyporus and Sepedophilus species generally have no secondary sexual characters or differences in genitalia of the type that might be used in specific mate recognition. Although one Australian species of Sepedophilus has abdominal peg setae. In studies on British Sepedophilus Hammond (1972) showed morphometrically that although the male genitalia are superficially very similar, their length and form is particularly constant and characteristic in each species.

Tachinus Gravenhorst

Tachinus species occur in a mixture of habitats, the majority being inhabitants of litter and moss but not of putrifying biotopes. Generally, in these cases there are poor genital differences between species, but there is constancy of form as in Sepedophilus. Good secondary sexual character differences are apparent in those species which do occur in habitats of the putrifying type, and where closely related species cohabit. Some of the features however, although striking, are associated with co-adaptation of males and females.

Fig.4.60 Abdominal features of Bolitobius; B.analis a) ventral view female, b) ventral view male; B.cingulatus c) ventral view male, d) ventral view female.

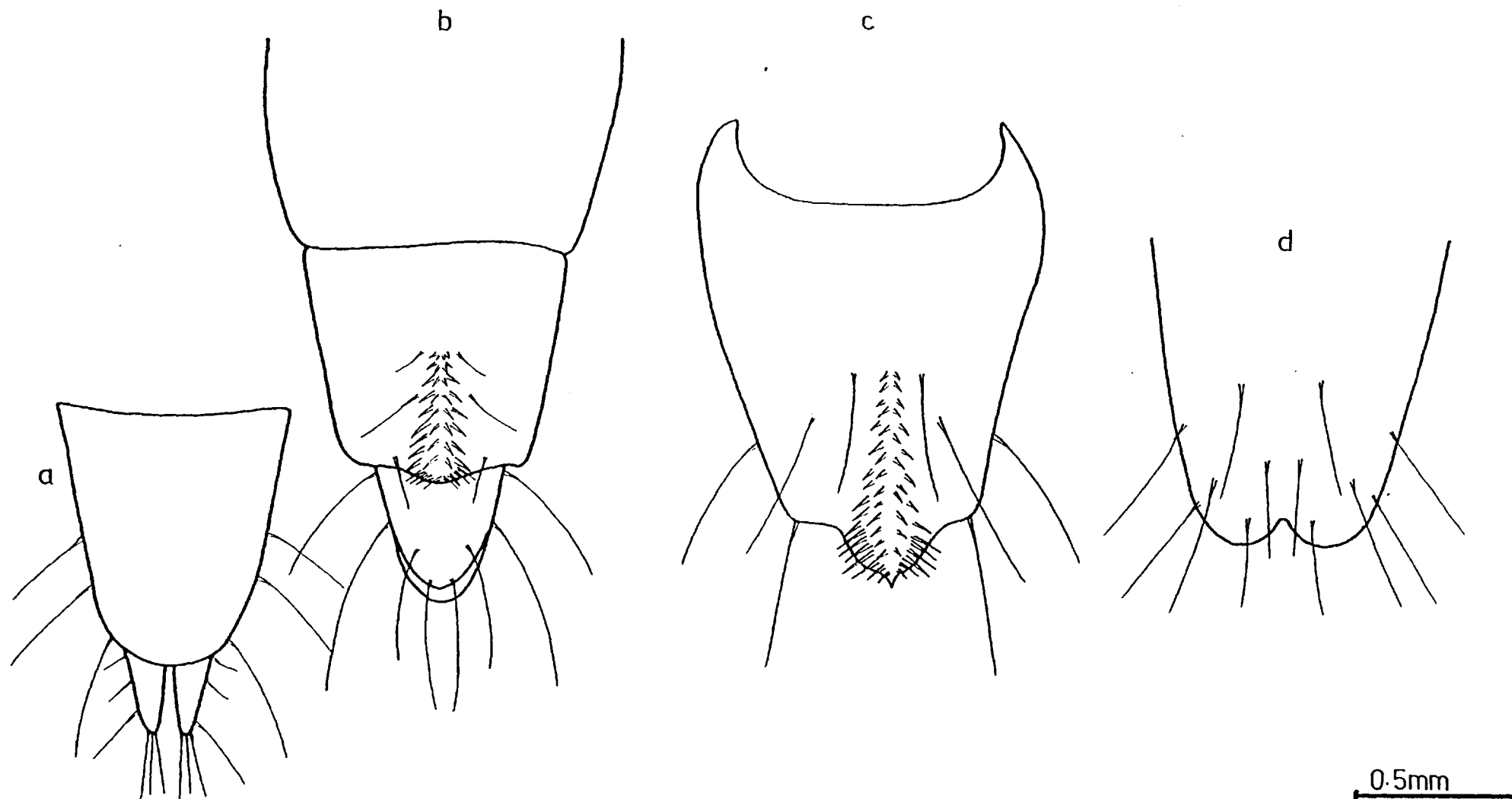
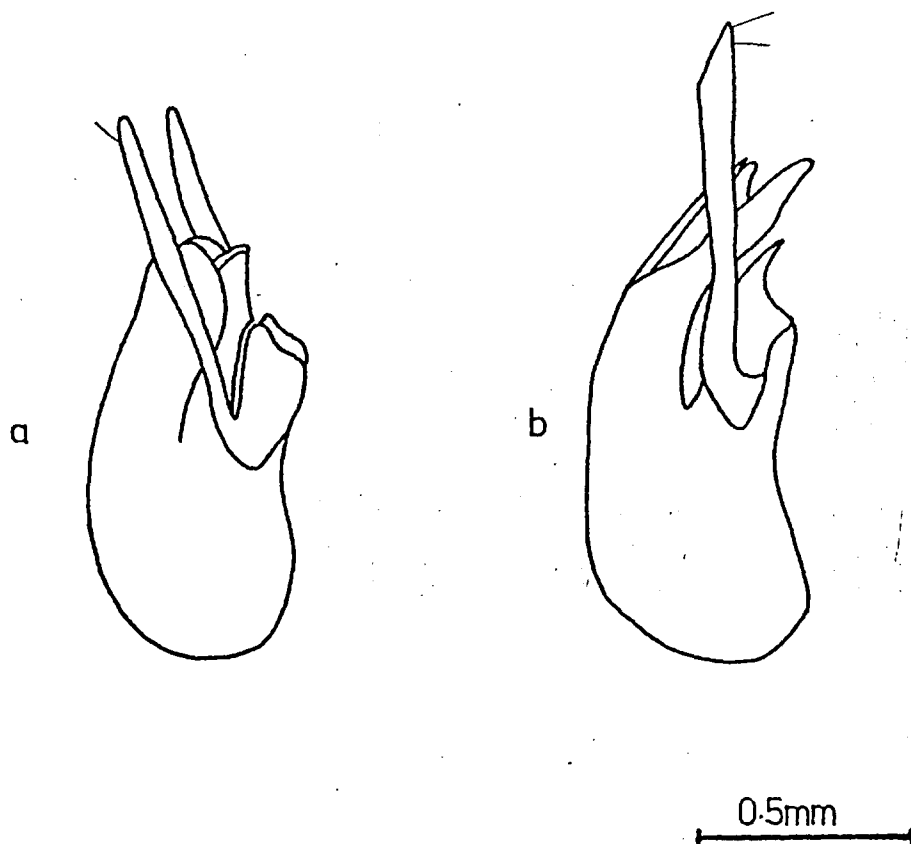


Fig.4.61 Male genitalia of Bolitobius; a) B.analis, b) B.cingulatus,



Secondary Sexual Characters

The pygidium (VIII) is variously lobed with arrangements of setae, in both sexes. The sternite of the propygidium (VII) is very characteristically modified in the males with patterns of peg setae; this is almost unique in the Tachyporinae (c.f. Sepedophilus).

The aedeagus is very stable within the genus but does show some constant inter-specific differences.

T. signatus group

T. flavolimbatus Pandelle

T. humeralis Grav.

T. laticollis Grav.

T. marginellus Fabricius

T. pallipes (Grav.)

T. proximus Kraatz

T. signatus Grav.

T. humeralis and T. proximus are very closely related and are often confused. T. signatus is close to T. pallipes. T. flavolimbatus is very close to T. marginellus and, to a lesser extent, to T. laticollis (Steel, 1961). All three species can be found syntopically.

Distribution and Habitat

Details are given by Horion (1967).

T. flavolimbatus

Western Mediterranean area; sporadic in western central Europe; western Africa.

T. humeralis

West and central Europe, and sporadic in occurrence in southern Europe; Siberia.

T. laticollis

Palearctic: Europe and Siberia.

T. marginellus

Palaeartic: sporadic in southern Europe; Siberia.

T. pallipes

Palaeartic, Europe (to the extreme north and south to the Pyrenees), Caucasus, Siberia and north America.

T. proximus

North and central Europe, Caucasus, and north-west America.

T. signatus

Palaeartic, Caucasus, Siberia and north America.

The British distribution of T. signatus, T. pallipes, T. humeralis, T. laticollis and T. marginellus is similar, each species being common and widespread. T. proximus is restricted to the northern half of England and Scotland, and T. flavolimbatus is sporadic in occurrence with records in Essex, Cambridgeshire, Kent and Norfolk (BMNH).

The habitats of the species are similar. They occur in dung, rotting fungus, nests of mammals (mainly in the dung). In addition, T. laticollis has been recorded from tree sap in spring, but may be more often in general litter, and T. flavolimbatus is found in decaying grass (also T. pallipes), haystack refuse, and fungus on elm (Steel, 1961). T. proximus and T. humeralis are syntopic, as are T. pallipes and T. signatus, and all four may be taken together. T. flavolimbatus, T. laticollis and T. marginellus occur in similar habitats and may be taken together.

Secondary Sexual Characters (terminology from Campbell, 1973 , also see Ullrich, 1975).

T. signatus and T. pallipes compared.

Pygidium (VIII): (Fig. 4.62 a & b and 4.63 a & b, Plate 4.6).

Fig.4.62 Male abdominal segments of Tachinus pallipes; a) tergite VIII, b) sternite VIII, c) sternite VII.

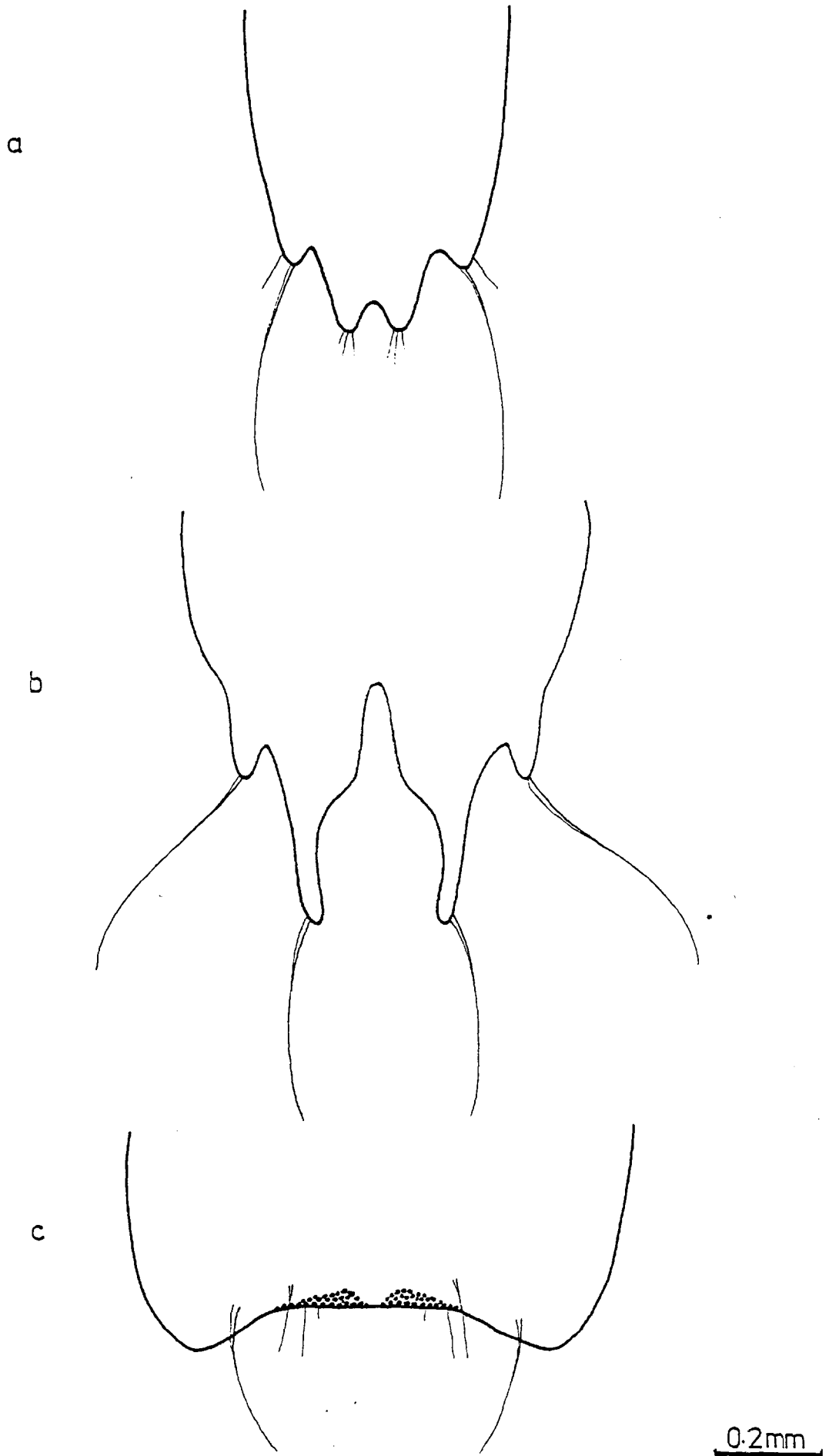


Fig.4.63 Female abdominal segments of Tachinus pallipes; a) tergite VIII, b) sternite VIII.

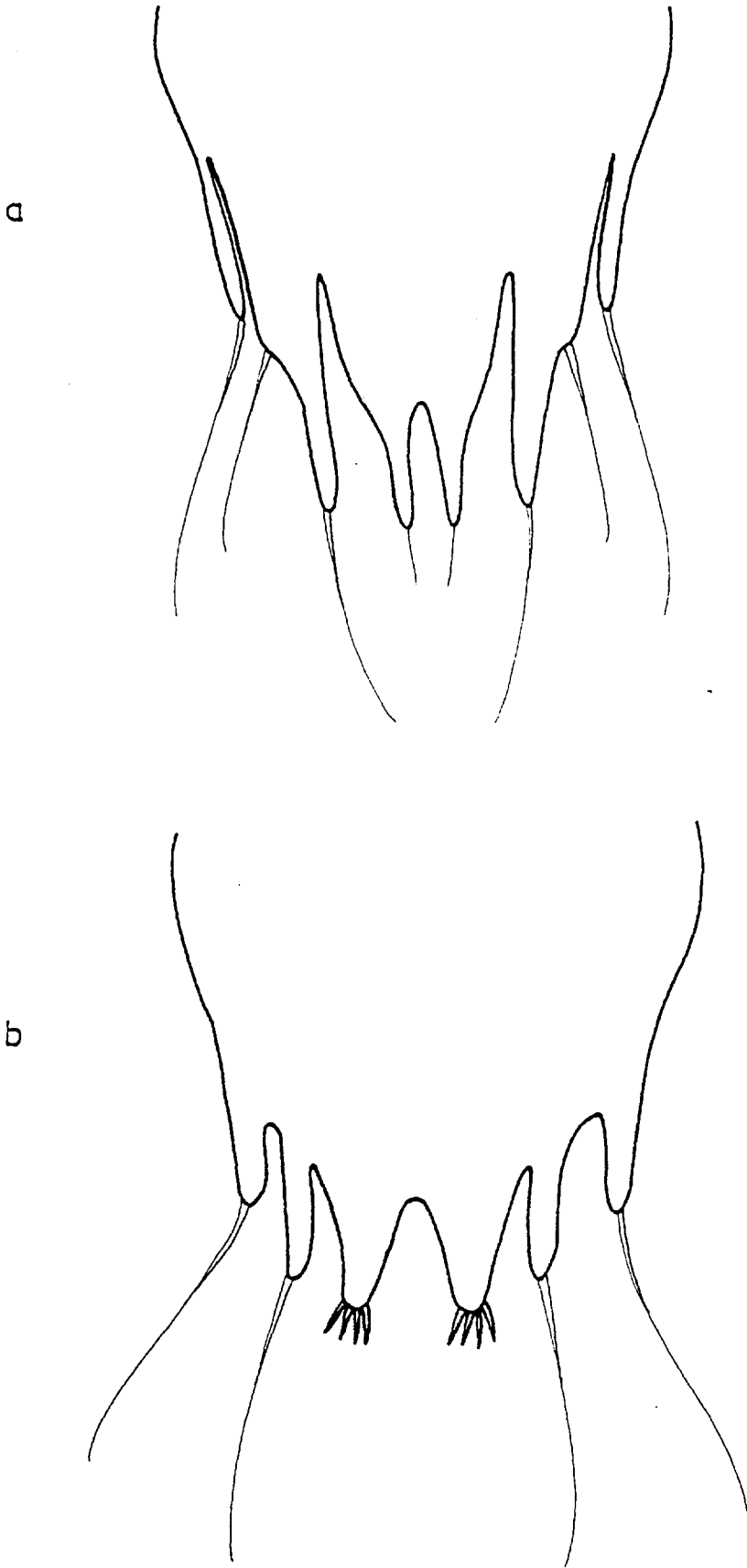


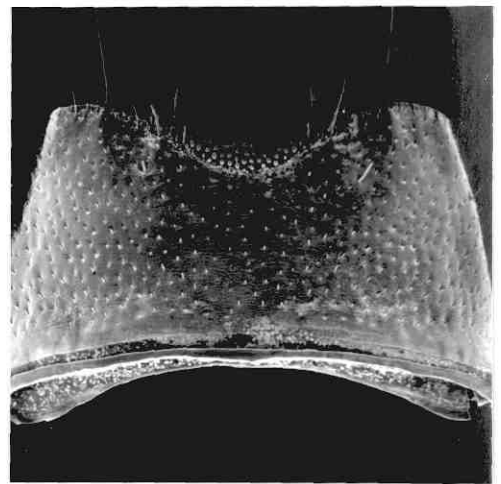
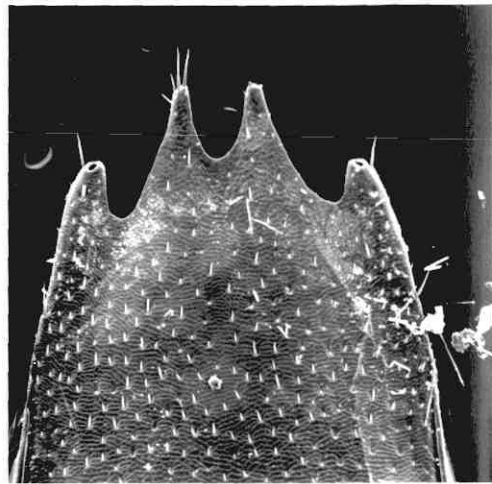
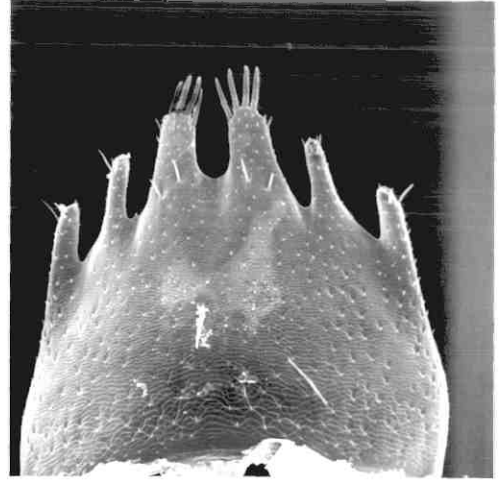
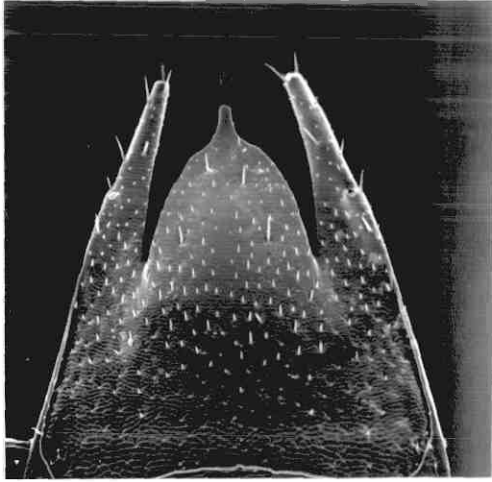
Plate.4.6. Scanning electron micrographs of abdominal sclerites of
Tachinus signatus.

a) Female tergite VIII (x 45)

b) Female sternite VIII (x 42)

c) Male tergite VIII (x 54)

d) Male sternite VII (x 42)



The tergite and sternite of the male are similar in both species. The female tergite is distinct. In T. signatus the central lobe tapers to the apex, while in T. pallipes it is deeply bilobed. The female sternite is also distinct in T. signatus with the fibriate lobes separated by a deep U-shaped emargination whilst T. pallipes has a further small lobe in the centre of the U.

Propygidium (VII) (Fig. 4.62 c).

The shape of the peg-pattern in the two species is distinct. T. signatus has a shallow semi-circular area of peg-setae, whilst T. pallipes has two small semi-circular areas of peg-setae at the posterior margin of the sternite.

T. humeralis and T. proximus compared.

Pygidium (VIII) (Fig. 4.64 a & b and 4.65 a, Plates 4.7 & 4.8).

The female sternites are similar in the two species, however, the female tergite and male tergite and sternite have quite distinct differences. (SEM observation of the internal surface of female pygidial sternite (VIII) in T. humeralis revealed an arrangement of tapering peg-like setae; interspersed with a series of rows of about 10 posteriorly directed spicules).

Propygidium (VII) (Fig. 4.64 c).

The differences in the seventh sternite are not substantial but they are constant in each species. In T. proximus the pegs form a shallow, semi-circular area along the post-margin of the sternite, and in T. humeralis they are similar but with the central anterior border indented.

T. flavolimbatus, T. laticollis and T. marginellus compared.

Pygidium (VIII) (Fig. 4.66 a, 4.67 a & b, 4.68 b, 4.69, 4.70 a & b, 4.71, Plate 4.8).

The female sternite, and the male sternite and tergite, are very

Fig.4.64 Male abdominal segments of Tachinus proximus; a) tergite VIII, b) sternite VIII, c) sternite VII.

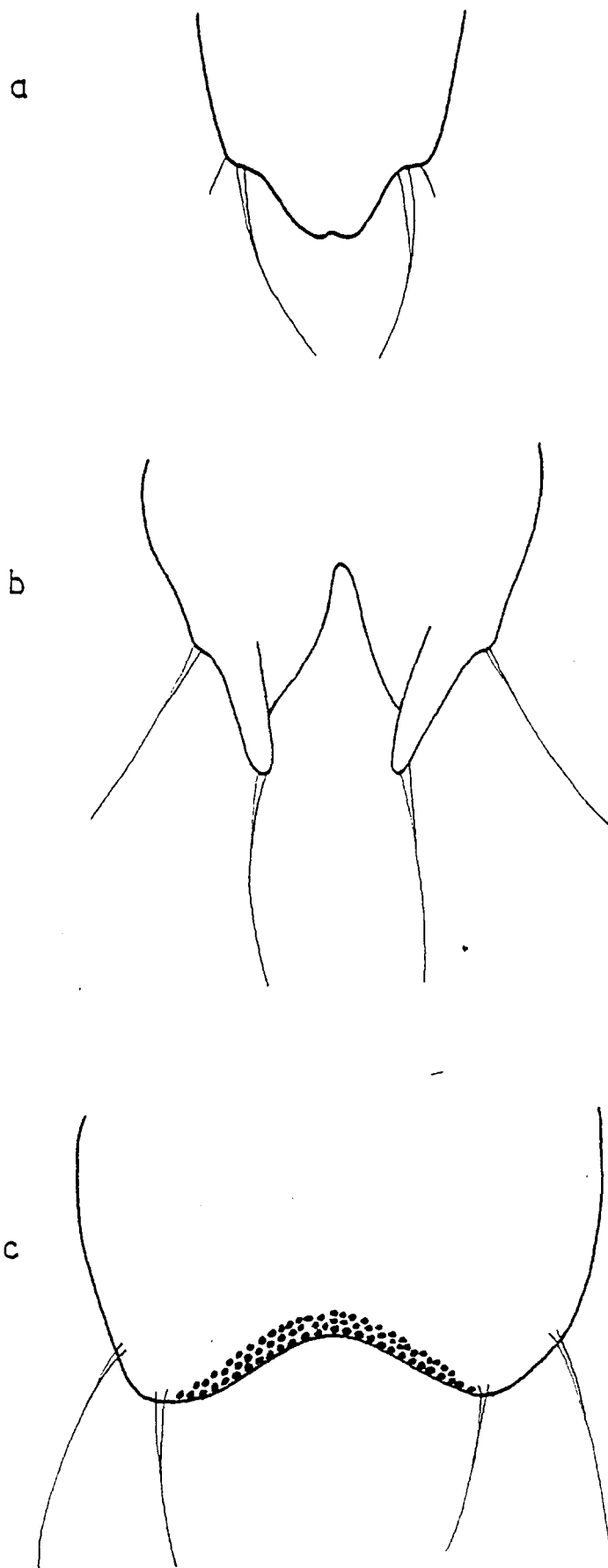
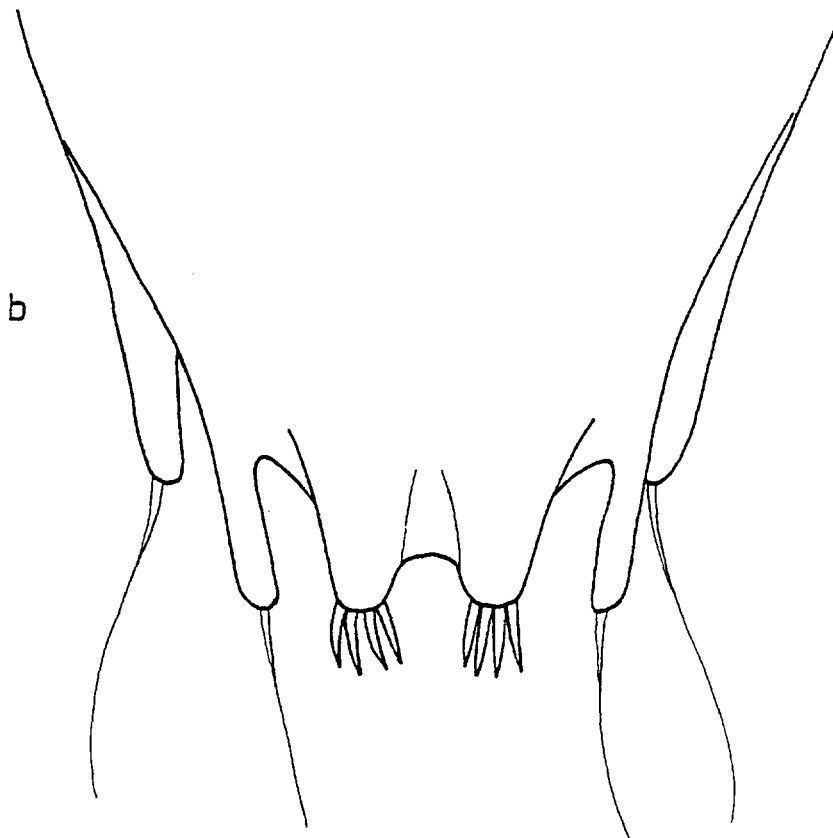
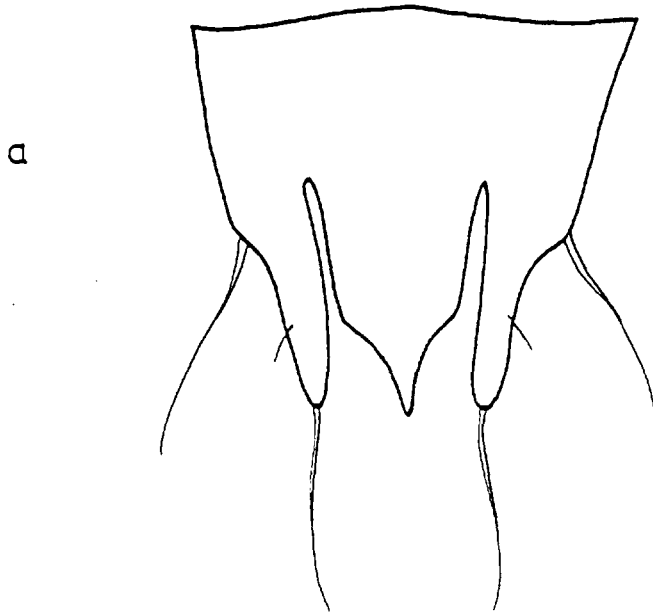


Fig.4.65 Female abdominal segments of Tachinus proximus; a) tergite VIII,
b) sternite VIII.



0.2mm

Plate.4.7. Scanning electron micrographs of abdominal sclerites of female Tachinus humeralis.

- a) Dorsal surface of sternite VIII (x 156)
- b) Dorsal surface of posterior border of sternite VIII (x 429)
- c) Dorsal surface of sternite VIII (x 1380)
- d) Elongate setae on posterior border of sternite VIII
(x 330)

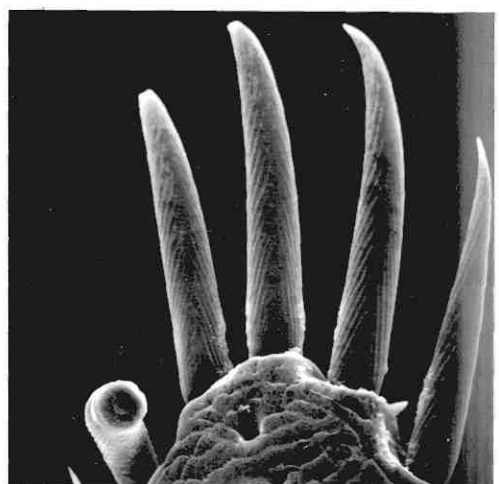
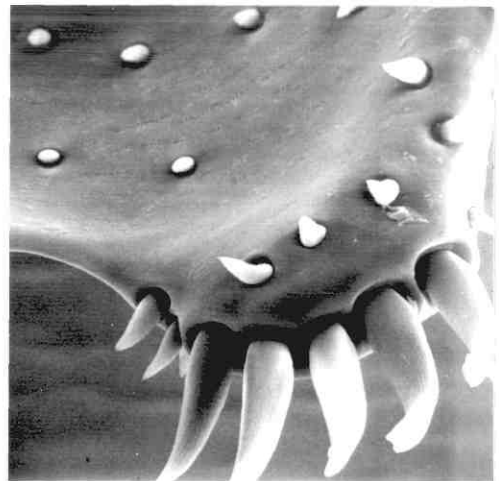


Plate.4.8. Scanning electron micrographs of abdominal sclerites of
Tachinus.

- a) T.laticollis, male sternite VII (x 78)
- b) T.humeralis, male sternite VII (x 33)
- c) T.humeralis, male sternite VIII (x 45)
- d) T.humeralis, male tergite VIII (x 42)
- e) T.humeralis, female sternite VIII (x 45)
- f) T.humeralis, female tergite VIII (x 57)

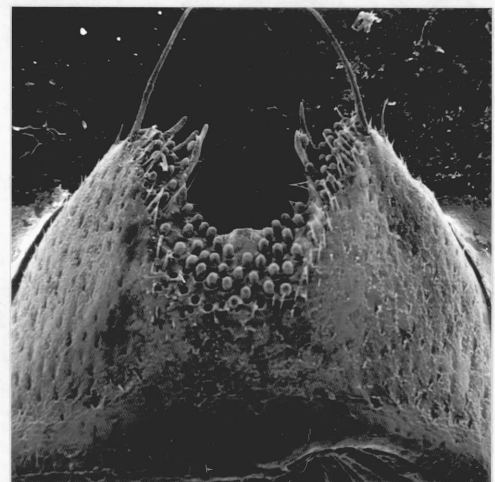
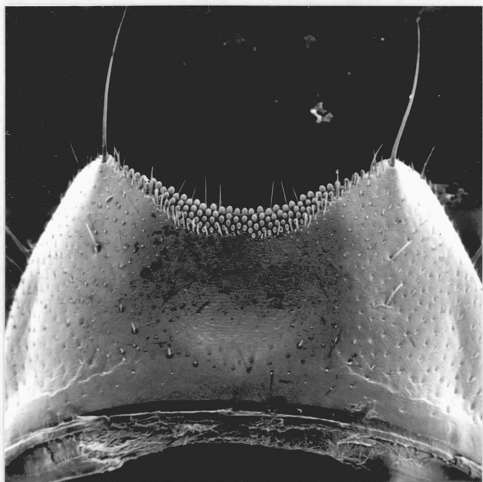
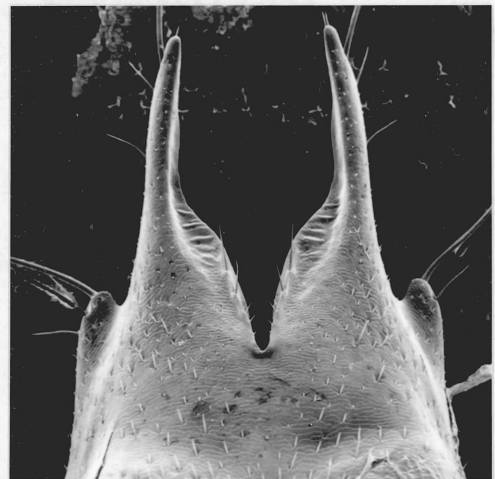
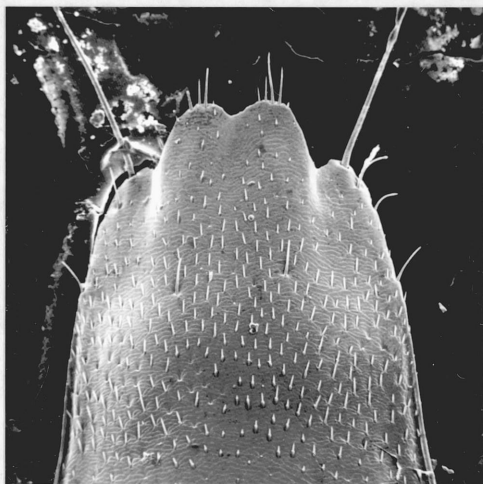
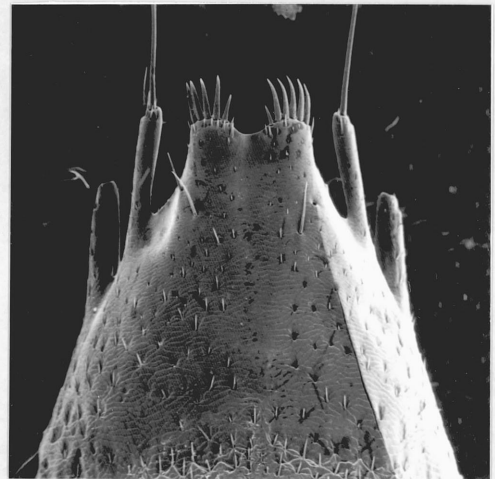
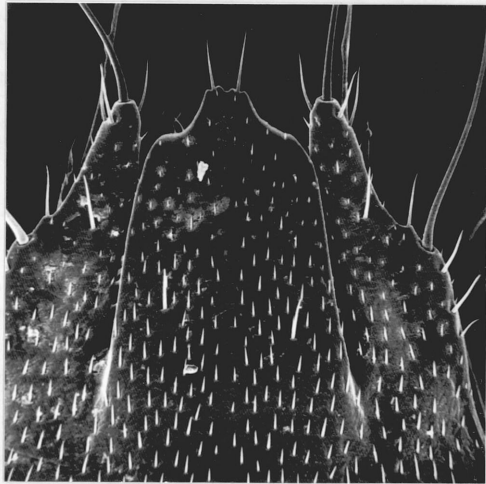


Fig.4.66 Male abdominal segments of Tachinus flavolimbatus;
a) sternite VIII, b) sternite VII.

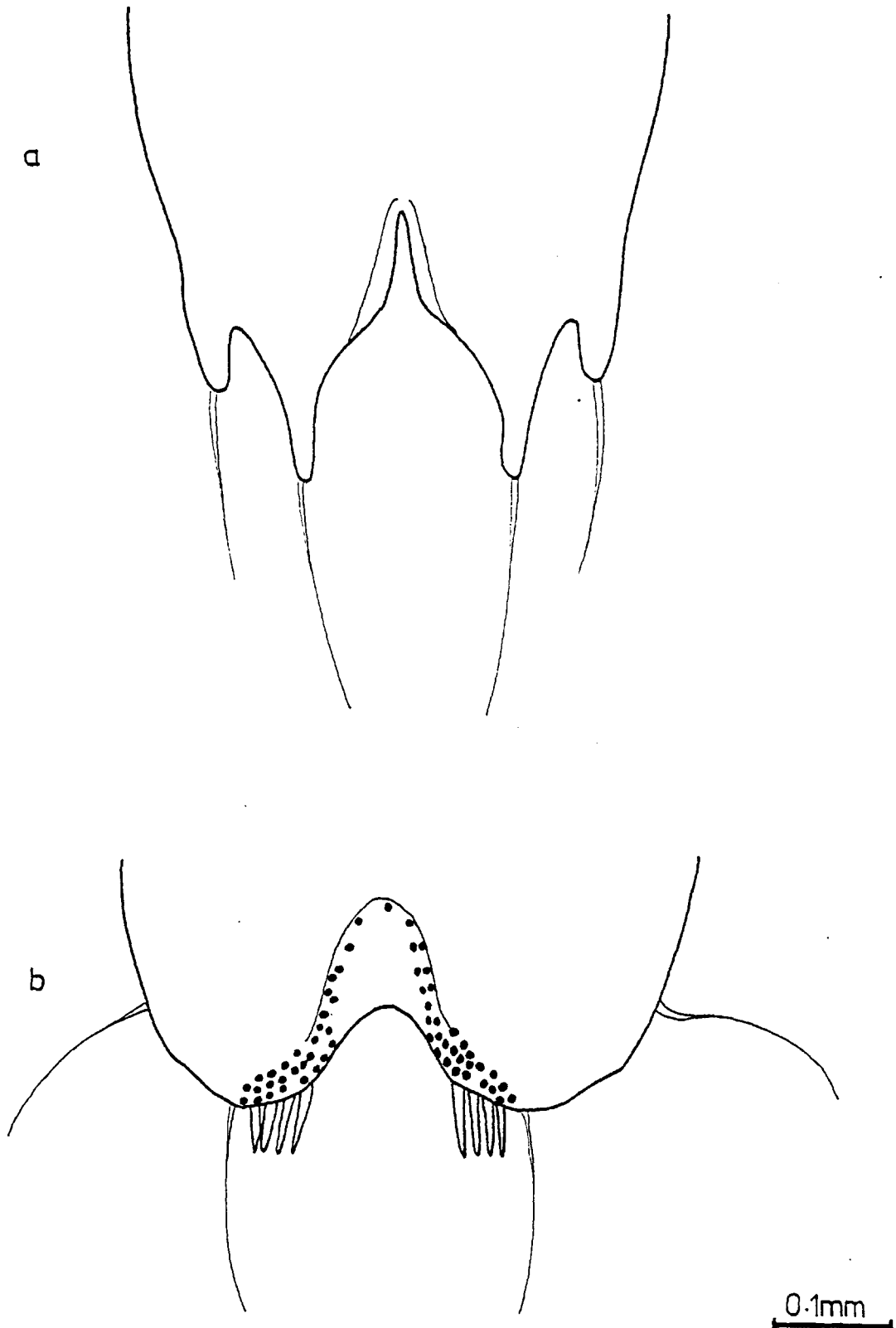


Fig.4.67 Female abdominal segments of Tachinus flavolimbatus;

a) tergite VIII, b) sternite VIII.

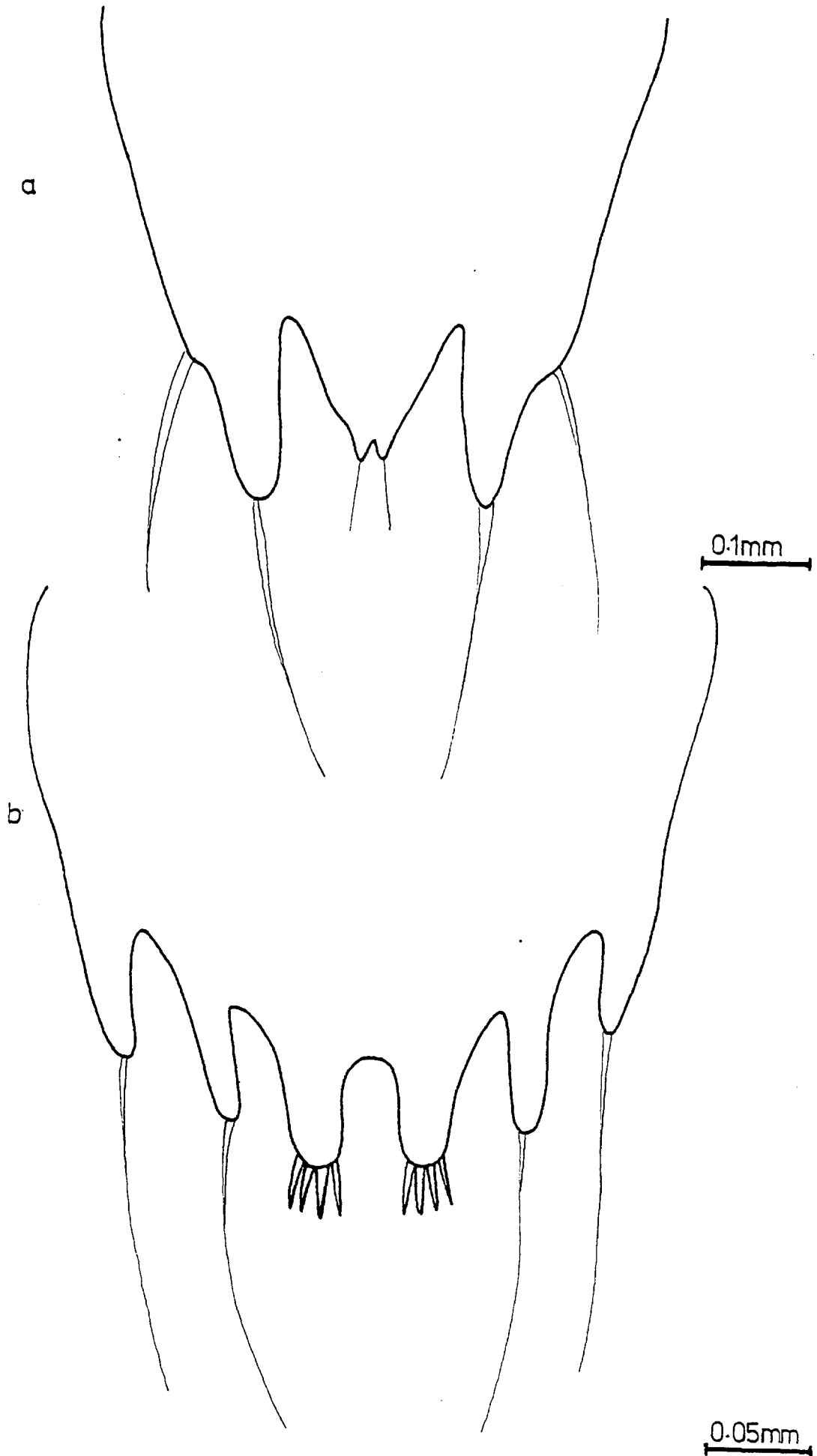


Fig.4.68 Male abdominal segments of Tachinus laticollis;
a) tergite VIII, b) sternite VIII.

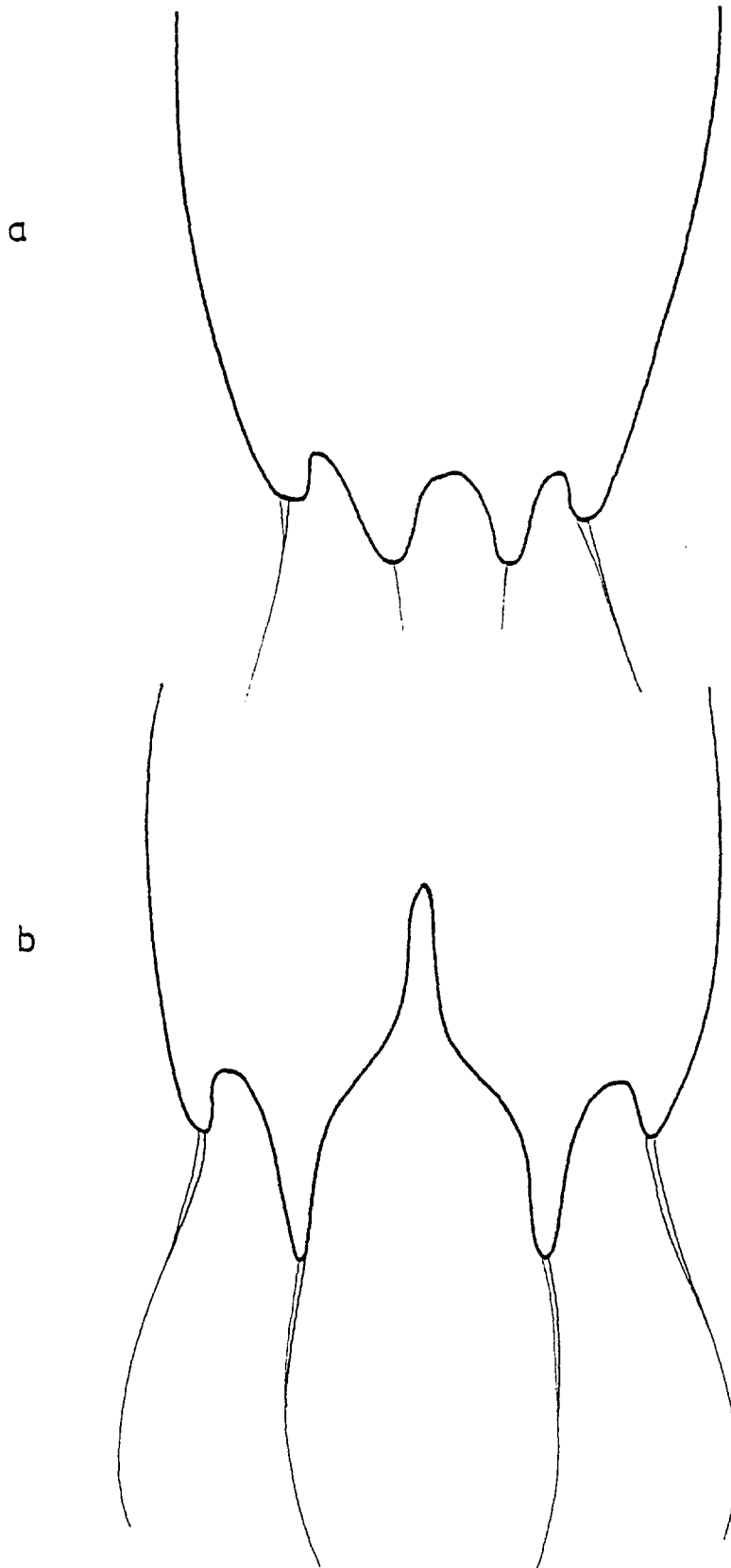


Fig.4.69 Female abdominal segments of Tachinus laticollis;
a) tergite VIII, b) sternite VIII.

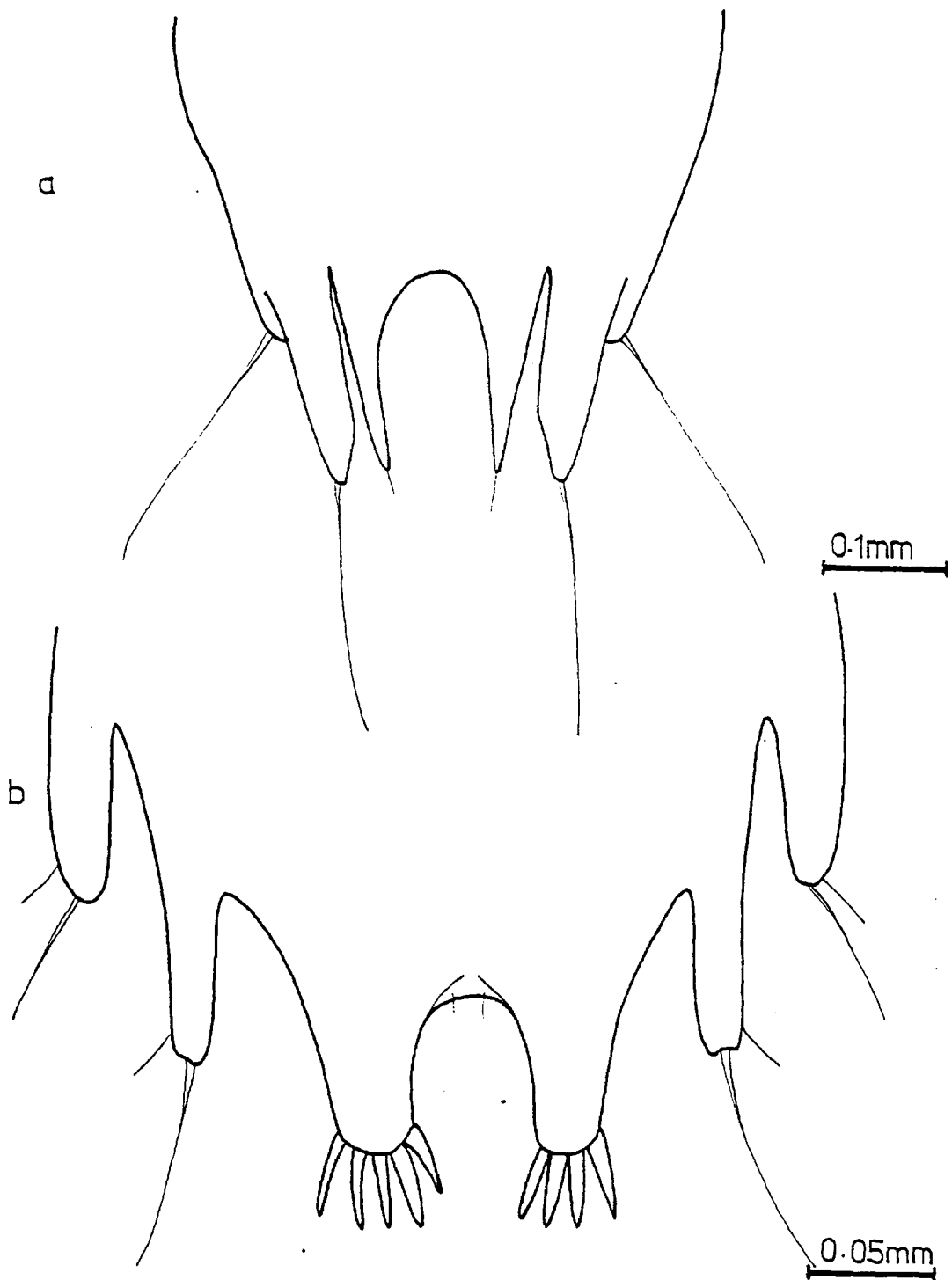


Fig.4.70 Male abdominal segments of Tachinus marginellus; a) tergite VIII, b) sternite VIII, c) sternite VII.

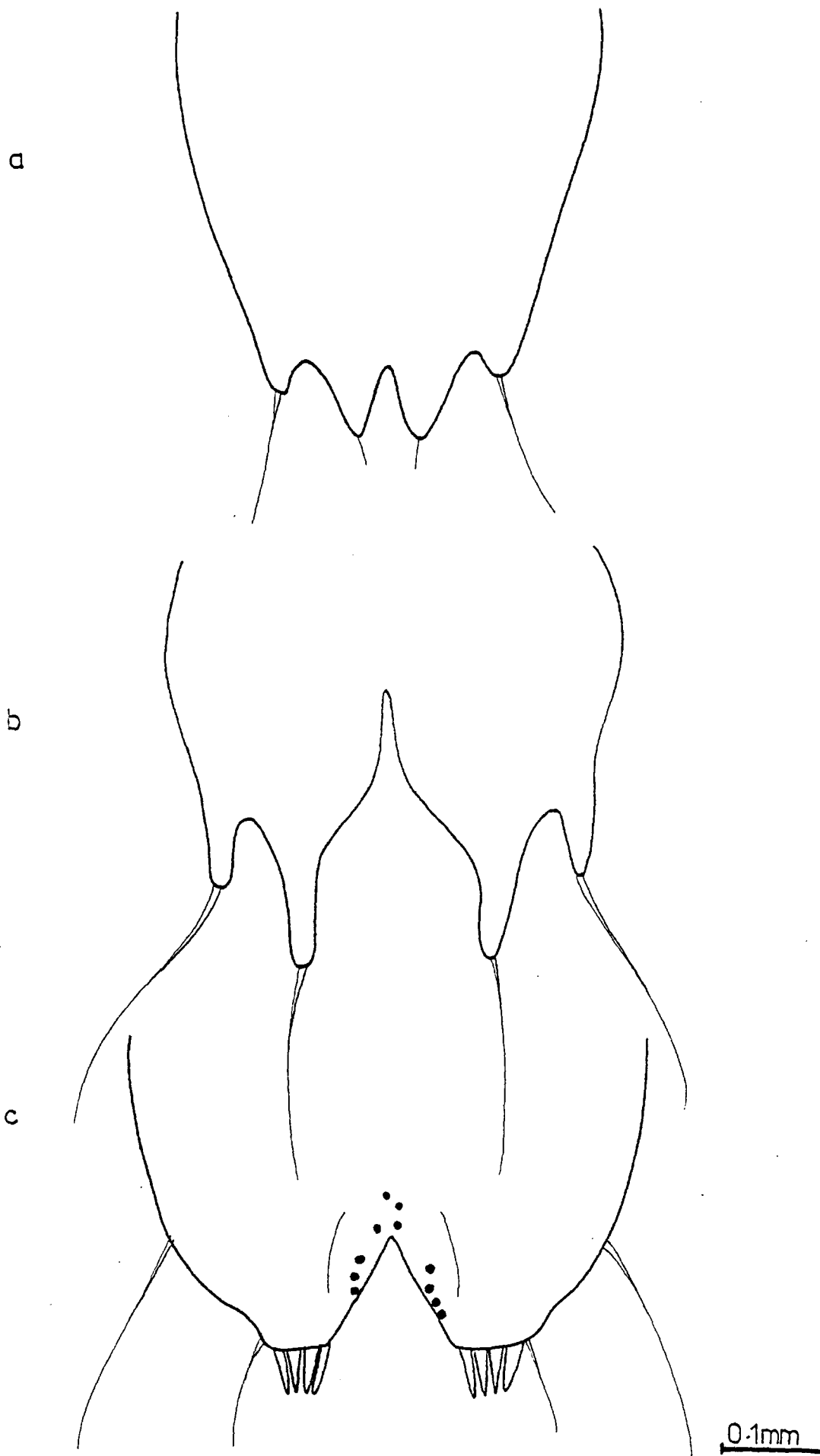
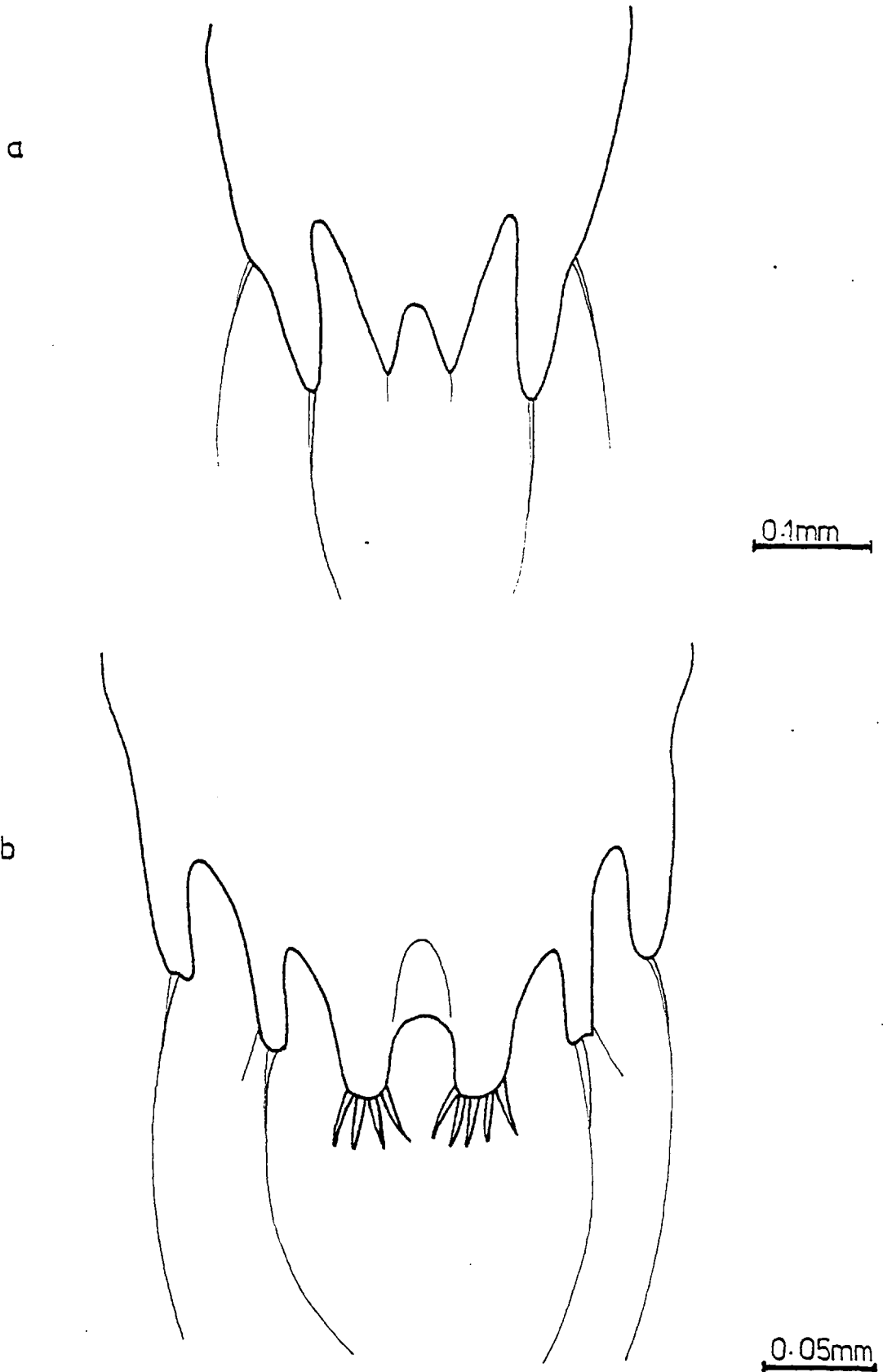


Fig.4.71 Female abdominal segments of Tachinus marginellus;
a) tergite VIII, b) sternite VIII.



similar in all three species.

The greatest difference is in the female tergite; whilst in T. flavolimbatus the central lobe is very slightly bilobed, in T. marginellus the central lobe is bilobed with a deep U-shaped emargination, and in T. laticollis the central lobe is deeply bilobed with a very deep U-shaped emargination.

Propygidium (VII) (Fig. 4.66 b and 4.70 c).

The three species have the same basic arrangement of secondary sexual characters although there are distinct differences. The emargination of the posterior margin of the seventh sternite is U-shaped in T. flavolimbatus and T. laticollis, but V-shaped in T. marginellus. The arrangement of peg setae around the emargination is distinct in the three species. In T. laticollis pegs cover the entire semicircular median impressed region around the emargination. In T. flavolimbatus there are peg setae around the lateral edges of the impressed region leaving the central area clear. In T. marginellus there is a central impressed region but there are only a few scattered peg setae.

To illustrate the exaggerated differences found in sympatric species in putrifying habitats, examples are taken from other closely related north American groups of species. These are illustrated by Campbell (1973).

1. T. memnonias-group.

The T. memnonias-group contains five species; T. memnonias Grav. from eastern north America, T. quebecensis Robert which is transcontinental, and T. semirufus Horn, T. rainieri Hatch and T. maculicollis Maklin from western north America.

T. memnonias and T. quebecensis are sympatric in the east, with T. quebecensis, occurring in decaying mushrooms. The two species have

been confused owing to their similarity. There are distinct differences in the male eighth sternite and female eighth tergite. The male seventh sternites have peg patterns and spiniform setae of a similar basic type, although their precise distribution is distinct.

T. semirufus is probably sympatric with T. quebecensis in the west, in rotting mushrooms and decomposing plant material. Differences occur in the female eighth sternite and tergite, and in the male eighth sternite. Substantial differences are exhibited in the male seventh sternite.

T. rainieri is sympatric with T. semirufus (but probably not with T. quebecensis) occurring in old bark, and debris at the base of trees. Differences are again apparent in the female eighth tergite and male eighth sternite. The patterns of peg and spinose setae on the male seventh sternite are of a similar type but show distinct differences.

T. maculicollis is sympatric with T. rainieri and T. semirufus. They occur in rotting fungi, carrion, and rotting vegetation. All three species are very similar, but distinct differences occur in the female pygidium and male seventh and eighth sternites. In T. maculicollis the seventh sternite is markedly different. Differences may also be exhibited by the chitinised armature of the internal sac.

2. T. fumipennis-group

Two north American species are of this group. The distribution of T. fumipennis (Say) includes north-eastern and mid-western United States, and south-eastern Canada, while T. axillaris Er. is from the south eastern United States. The pair are probably sympatric where their distributions overlap. T. fumipennis is recorded from decaying plant material, animal tissue, mushrooms, carrion, animal burrows and

dung. T. axillaris is recorded from carrion and litter. The eighth sternite of the male and the eighth tergite of the female exhibit differences, but the most striking distinction lies in the male seventh sternite. T. axillaris is completely lacking in peg or spinose setae, yet in T. fumipennis they are present.

3. T. luridus-group

The T. luridus Er. group contains four species occurring in rotting mushrooms, carrion and dung. T. luridus is from eastern north America, T. nigricornis Mann. (which may be a subspecies of T. luridus) is from west and central north America, and T. canadensis Horn from western north America. T. basalis Er. is from east and western north America, and records of specimens between these two populations are unknown. They exhibit a distinct size difference, and this may indicate that the two populations are subspecies.

T. luridus and T. nigricornis are close, but they are allopatric with very minor differences in their secondary sexual characters; however, the male seventh sternite is distinct. T. nigricornis and T. canadensis are sympatric with very distinct secondary sexual characters which includes the male propygidium. Similar distinction is seen between T. canadensis and T. basalis (western population).

There is no difference in secondary sexual characters between the east and west populations of T. basalis. T. basalis is sympatric with all three other species of the group, and the secondary sexual characters are very different from those of the others.

Variation

From an examination of different groups of species it is clear that the most uniform and constant structure throughout is the male pygidial tergite (VIII). The female pygidium and male pygidial sternite show distinct differences although the basic structure

remains similar. Much greater differences occur between, than within, groups of species.

Function

Mating behaviour has been observed in T. signatus although clear determination of the function of the secondary sexual characters was not achieved (Section 5.2.14). However, it appears that there is some co-adaptation in the shape of the male sternites and female tergites. During mating these are firmly clamped together. Prior to insertion of the aedeagus the female is palpated and antennated particularly around the abdominal apex, it is therefore likely that the structures of the female pygidial sternite are "examined" during this process. Likewise, on being mounted the female would have the opportunity to make contact with the male propygidial sternite.

It is very likely that these structure play a significant role in specific mate recognition since from the evidence obtained in observation of mating behaviour these structures were not observed to function in any other way.

4.3.7 Aleocharinae

Many groups of the Aleocharinae have acquired a mating position whereby the male abdomen is flexed dorsally over his head for insertion of the genitalia into the female genital orifice. (Section 5.5.2.6). This is most likely to be the reason for the dorsal siting of the male secondary sexual features which are apparently of the tactile recognition type, e.g. Gyrophæna.

Gyrophæna Mannerheim

G. affinis Mannerheim

G. angustata (Stephens)

G. fasciata (Marshall)

G. gentilis Erichson

G. minima Erichson

G. nana (Paykull)

G. pulchella (Heer)

Distribution and Habitat

Details are given by Horion (1967).

G. affinis

Palaeartic; North America, east Siberia.

G. angustata

Palaeartic; Europe, Caucasus, Siberia.

G. fasciata

North and central Europe; Caucasus.

G. gentilis

North and central Europe; Caucasus.

G. minima

North and central Europe.

G. nana

North Palaeartic; north and central Europe, Caucasus, Siberia.

G. pulchella

North Palaeartic: north and central Europe, Caucasus,
Siberia, North America.

With regard to their British distributions, they are all more or less widespread but local, except for G. angustata and G. pulchella which are south-eastern in distribution.

Gyrophæna species are specialist fungus dwellers in many unrelated species of Agaricales and Polyporaceae. Gyrophæna species tend not to be associated but occur widely on a range of different fungi. White (1977) lists host species for the twelve commonest Gyrophæna species in Great Britain. Numbers of species are,

however, found together, the Tricholomataceae and Cortinariaceae being the most common hosts. Some common hosts are :-

G. affinis: Numerous species, e.g. Amanita rubescens, Collybia sp.
Pholiota mutabilis, Polyporus squamosus.

G. angustata: Tree fungi, e.g. Polyporus, Trametes, Fomes, Pholiota etc.

G. fasciata: Numerous species, e.g. Polyporus squamosus, Pholiota sp.

G. gentilis: Diverse species, e.g. Collybia platyphylla.

G. nana: Tree dwellers e.g. Polyporus squamosus.

G. pulchella: Tree dwellers e.g. Clytocybe and Collybia sp.

Hence G. affinis, G. fasciata and G. nana are likely to be syntopic (possibly also G. angustata), as are G. affinis, G. gentilis and G. pulchella.

Secondary Sexual Characters

Gyrophæna species are closely related to one another and the most reliable means of identification is by the male characters of the dorsal surface of the hind abdomen.

Tergite VII: (Fig. 4.72).

Raised cuticular protrusions may be present towards the posterior margin.

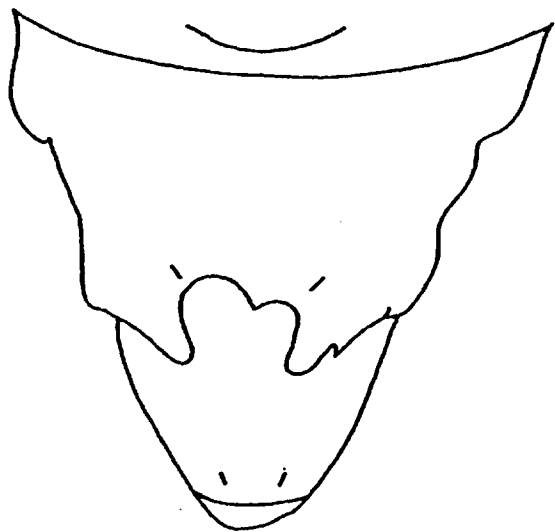
Tergite VIII: (Fig. 4.72)

Raised cuticular protrusions of a similar type to TVII may be present towards the posterior margin. The posterior margin is emarginate, either simply as in G. fasciata, or with two widely spread lobes separated by a simple or asymmetrical U-shaped space as in G. pulchella, G. affinis, and G. angustata; or with two lateral and two central lobes e.g. G. minima, G. gentilis, and G. nana.

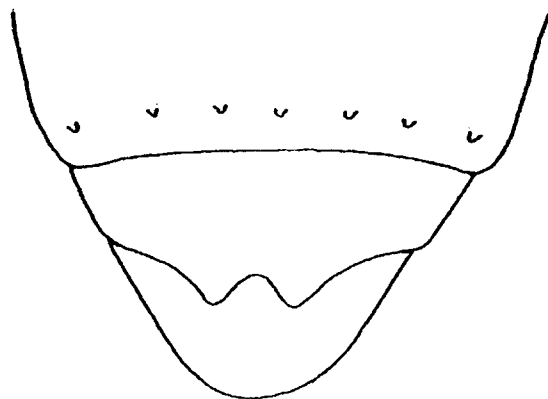
Fig.4.72 Male abdominal segments of Gyrophæna (tergites VII & VIII)

- a) G.pulchella, b) G.fasciata, c) G.gentilis, d) G.nana,
e) G.angustata, f) G.affinis, g) G.minima.

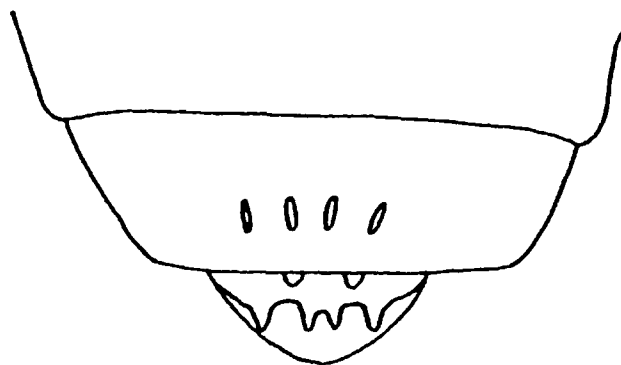
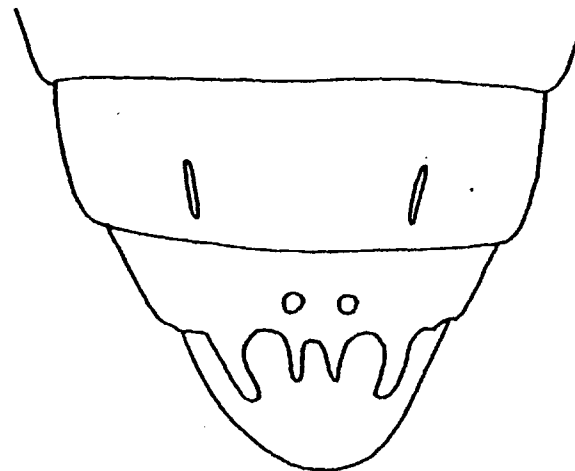
a



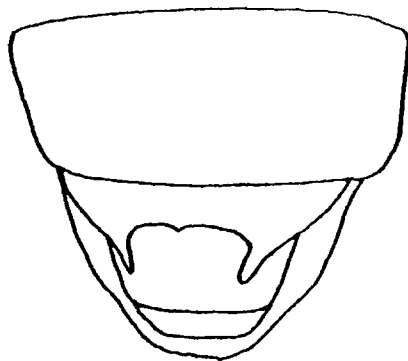
b



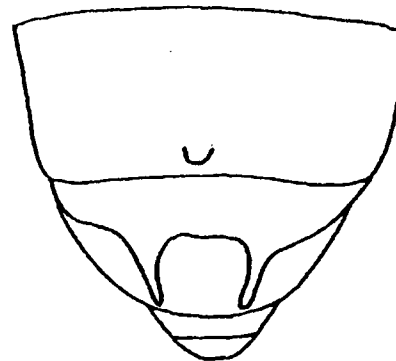
c



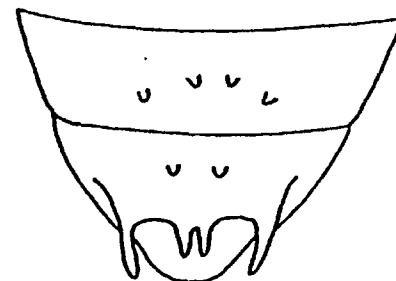
d



e



f



g

0.2mm

Aedeagus: (Figs. 4.73 and 4.74)

The genitalia are remarkably distinct in all the species, with an enormous difference in size. G. affinis and G. minima, and G. nana and G. angustata are of comparable size, while G. gentilis, and G. pulchella have increasingly larger genitalia.

Function

It is not known whether the remarkable differences in the structure of the median lobe are in any way concerned with reproductive barriers, such as mechanical isolation. The lateral lobes are of a similar form in all the species and are used to grip the female abdomen during mating.

Aleochara Gravenhorst

A. bilineata Gyllenhal

A. bipustulata (Linnaeus)

A. curtula (Goeze)

A. lata (Gravenhorst)

Distribution and Habitat (Horion, 1967, and Welch, 1964).

A. bilineata

Holarctic: Europe, Caucasus, Asia Minor, North America, Canada, U.S.A., Madeira, etc.

A. bipustulata

Palaearctic and Nearctic: Canada, U.S.A., Africa, Madeira etc.

A. curtula

Palaearctic: North and South America.

A. lata

South Palaearctic: west, central and southern Europe, Asia Minor, Caucasus, Siberia, North America, Chile.

A. bipustulata is common and widespread in the British Isles and found chiefly in carrion but also in flood refuse and moss.

Fig.4.73 Male genitalia of Gyrophæna; a) G.pulchella, b) G.fasciata.

i. lateral view, ii. lateral view lateral lobe.

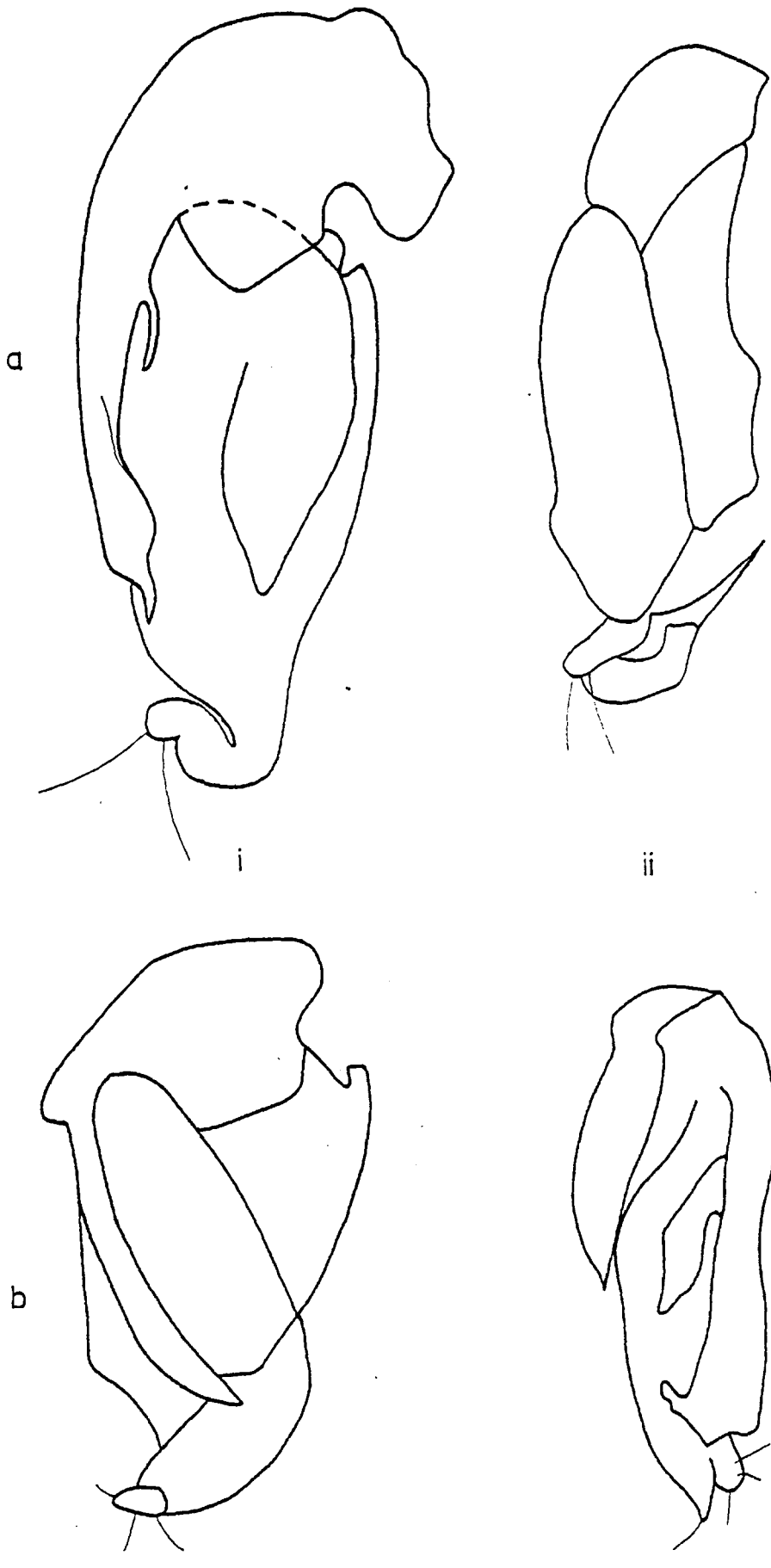


Fig.4.74 Male genitalia of Gyrophaena; a) G.nana, b) G.angustata,
c) G.affinis, d) G.minima (i. mid piece, ii. lateral lobe).



A. bilineata is locally distributed extending to northern Scotland and occurs in dung, haystack refuse, seaweed and mammals nests.

A. curtula is the commonest carrion species and is probably distributed all over Britain. There are a few records from habitats other than carrion; such as fungi, moss and nests.

A. lata is found almost exclusively on carrion in association with A. curtula but is less common. A. lata is found north to Notts. and there are no Irish records. (Distribution maps are given in Welch, 1964).

Secondary Sexual Characters

There are no abdominal secondary sexual characters.

Genitalia and Function:

There are distinct differences in the genitalia (Figs. 4.75 - 4.78) particularly in the apical part of the median lobe which is thought to be coadapted with the female genitalia (Peschke, 1978a).

Section 5.5.2.6). The lateral lobes are of a more uniform type, and are used to clasp the female abdomen tip during mating.

The lack of features of a type which could be involved in recognition, may be due to the production of a female sex pheromone. The pheromone triggers the grasping reaction of male lateral lobes in A. curtula (Peschke, 1978b) and possibly the other species (Section 5.5.2.6).

4.3.8 Pselaphidae.

The Pselaphidae are closely related to the Staphylinidae, and any phylogenetic classification would include them in the Staphylinidae. They are particularly close to the Steninae (Crawson, 1954; 1967).

Their habitats are generally moist and dark including thick, deep, damp mosses; around bases of trees and grass tussocks; decaying vegetable refuse, manure and straw heaps, flood refuse, litter, under thick bark and in rotten wood. One family is entirely

Fig.4.75 Male genitalia of Aleochara bilineata; a) dorsal view,
b) lateral view, c) lateral lobe.

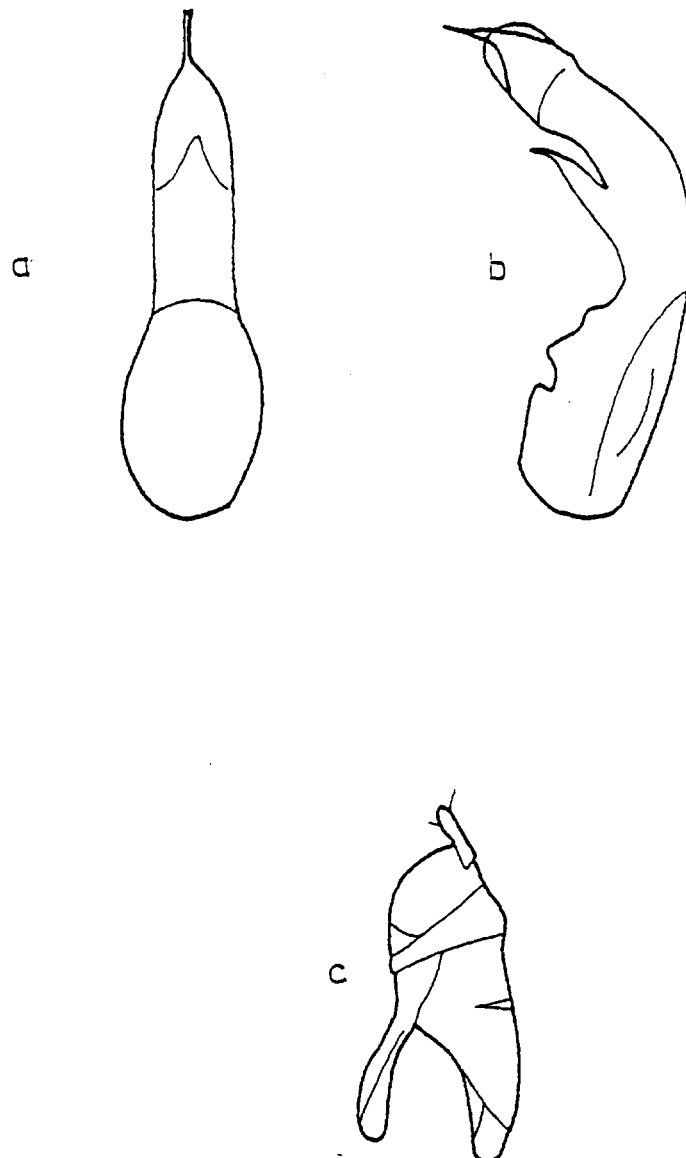


Fig.4.76 Male genitalia of Aleochara bipustulata; a) dorsal view,
b) lateral view, c) lateral lobe.

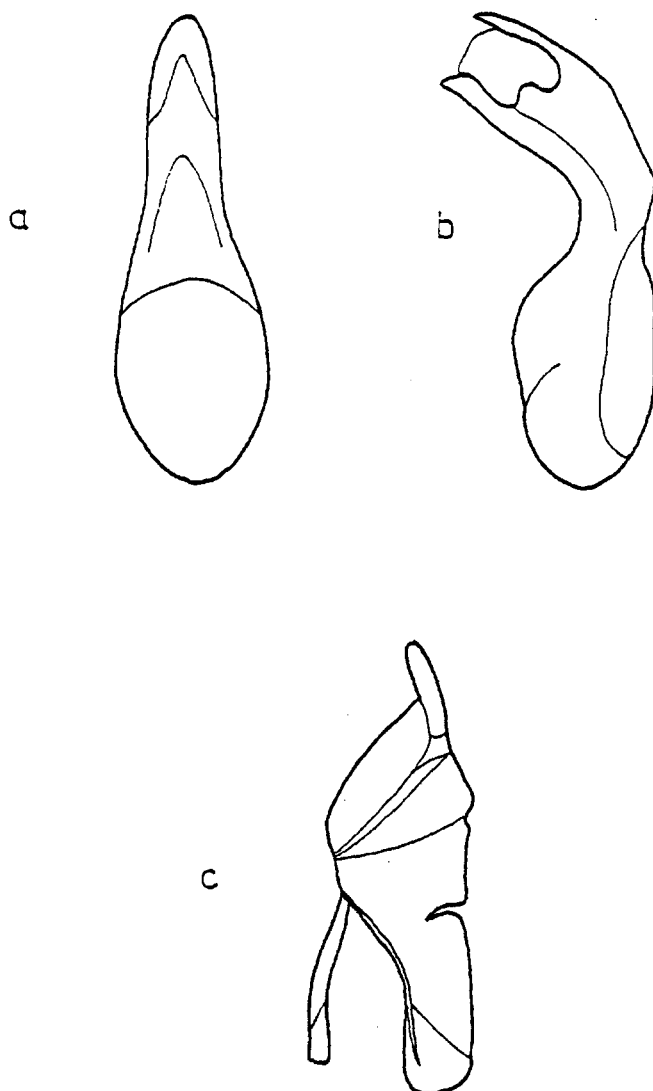


Fig.4.77 Male genitalia of Aleochara curtula; a) dorsal view, b) lateral view, c) lateral lobe.

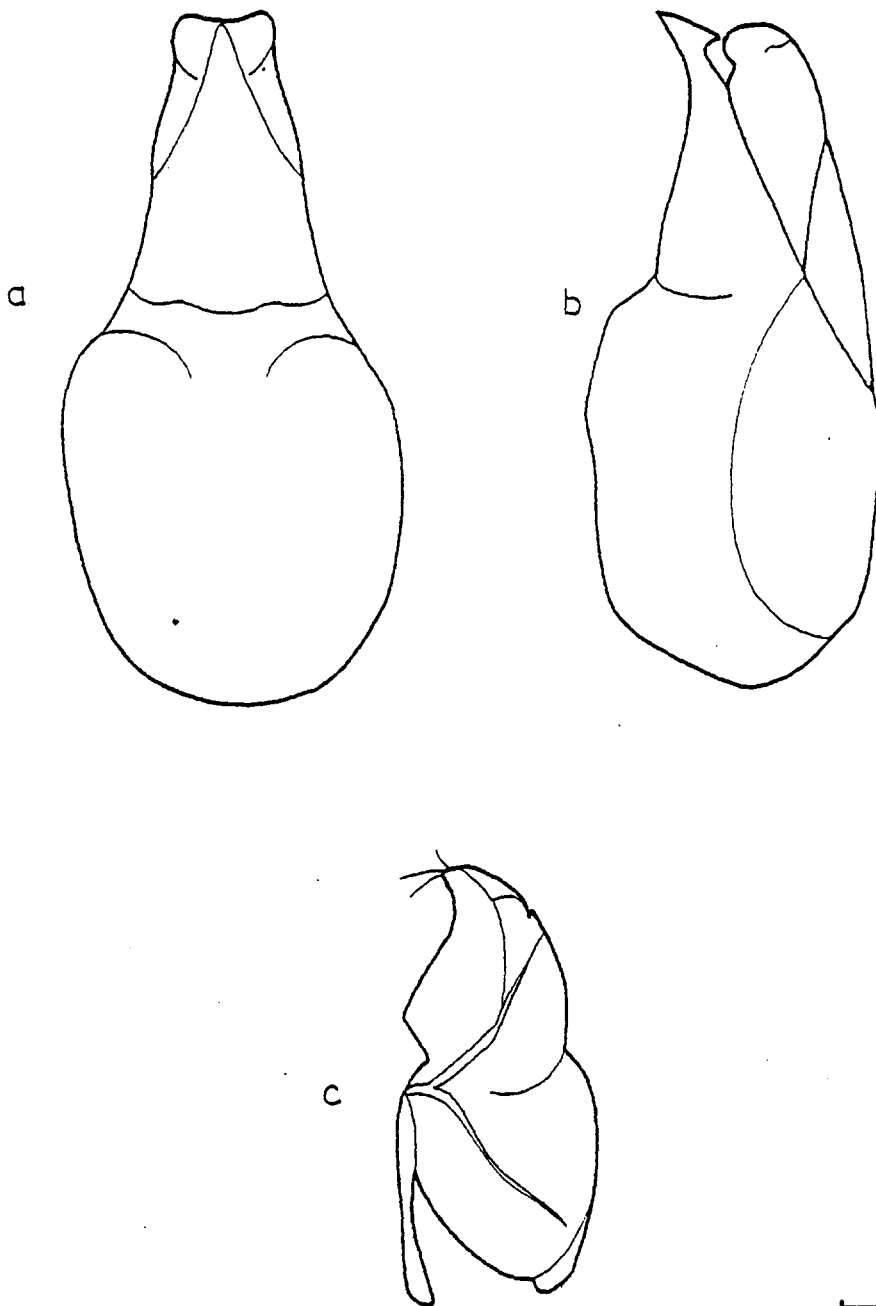
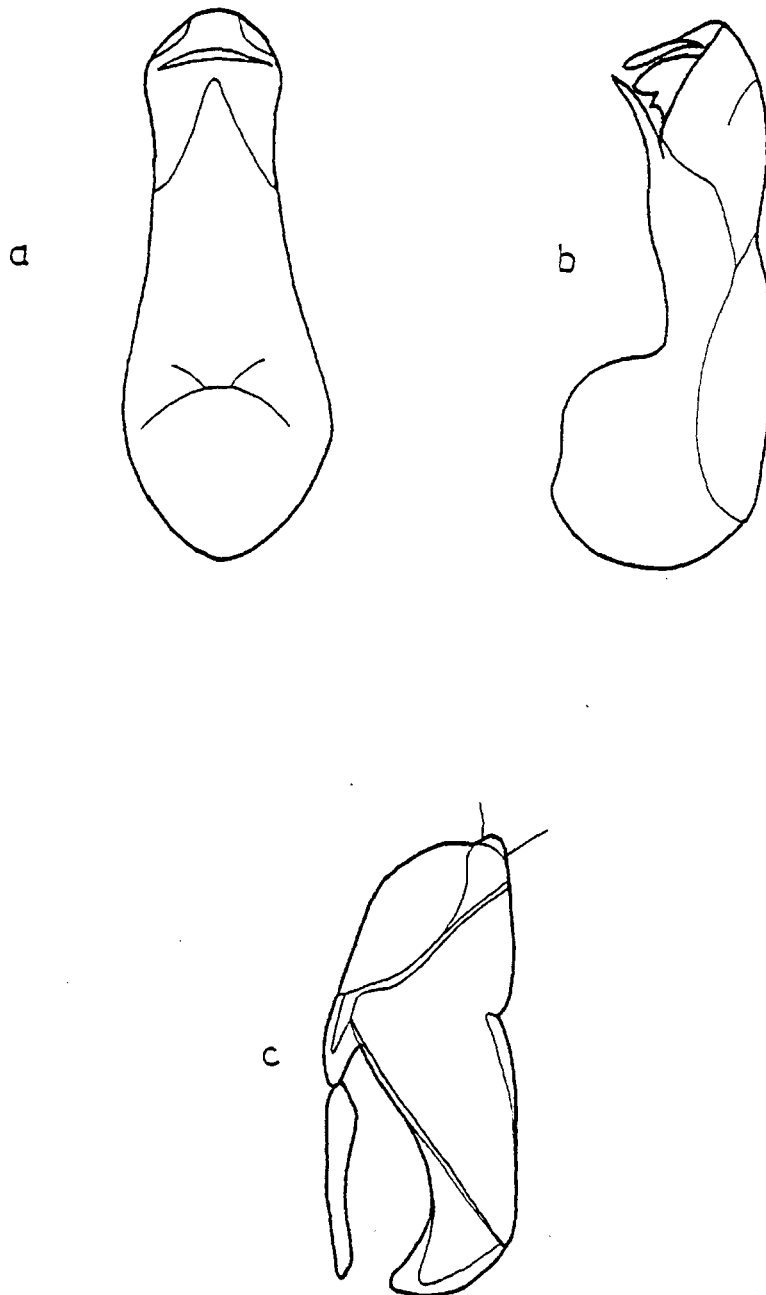


Fig.4.78 Male genitalia of Aleochara lata; a) dorsal view, b) lateral view, c) lateral lobe.



myrmecophilus (Pearce, 1957).

The family is notable for its extreme diversity of form. In many genera the secondary sexual characters of the males are very pronounced; either owing to the great development of certain segments of the antennae or maxillary palps, or to the possession of conspicuous spines or spurs on the mid and hind legs. In some genera the mid-femora are noticeably thickened.

The Pselaphidae have encapsulated aedeagi; the tegmen forms a basal capsule in which the median lobe, which may be very reduced and membranous, is represented only by the internal sac. The resulting structure is highly complex with the added complication of the existence of polymorphism amongst males which, very often, takes the form of inversions of the aedeagus. Inversions involve structural mutations arising in the construction of the individual or species and often occur in asymmetrical genitalia. The structure of the aedeagus is altered so that the physiological and morphological characters are transposed (Jeannel, 1955). In subfamilies where the aedeagus is symmetrical e.g. Bryaxitae and Pselaphitae, inversion occurs in the transportation of the structures of the internal sac.

The family is utilised to illustrate the extreme lability of the aedeagus, and exposes the case of sympatric males with polymorphic genitalia. Freude, Harde & Lohse (1974) regard cases of inversions and polymorphisms warranting subspecific status.

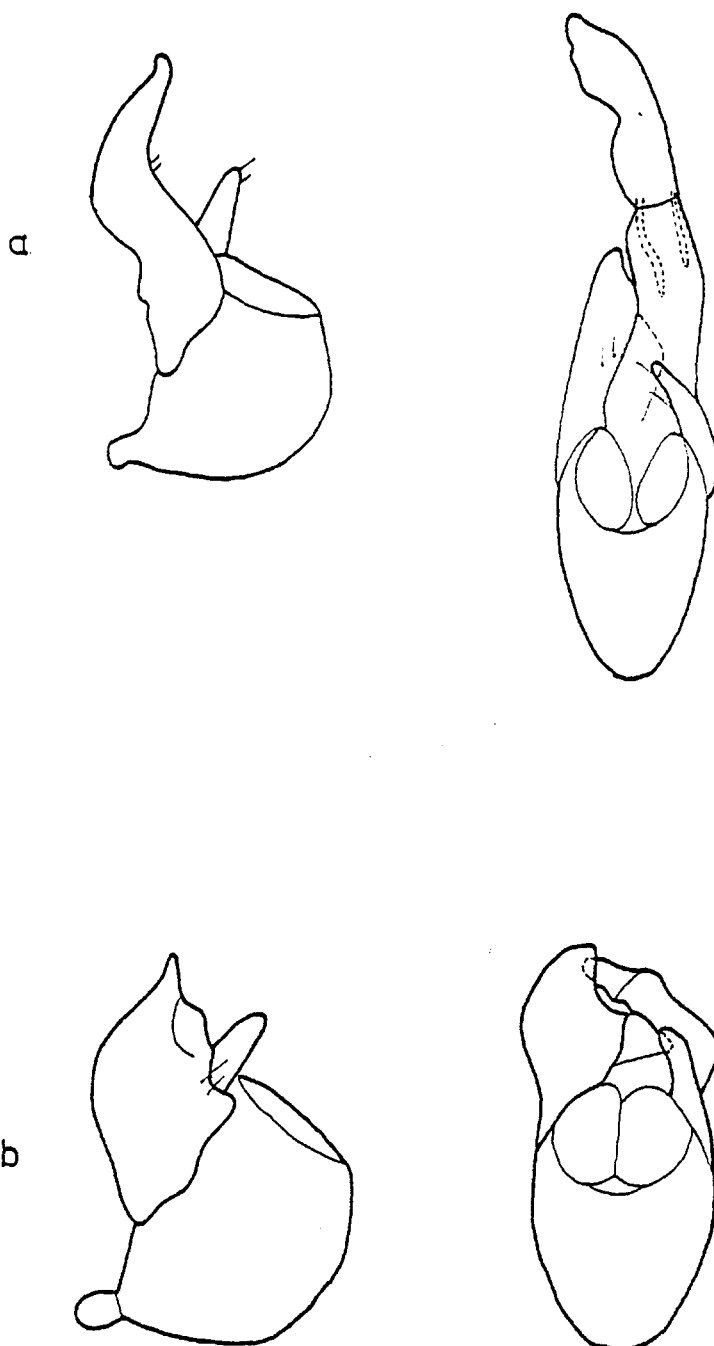
Examples

1. Close sympatric species

Bibloporus minutus Raffr. and B. bicolor (Denn.)

The pair are sympatric under bark. In external morphology they are very similar, the females being almost inseparable. The males differ in characters of the mesotibia and femur, and the aedeagus (Fig. 4.79) (Steel, 1963).

Fig.4.79 Male genitalia of Bibloporus; a) B.minutus, b) B.bicolor,
(after Steel, 1963).



2. Inversions of the aedeagus

- a) Euplectus kirbyi revelierei Reitt. (Fig. 4.80 a).

E. kirbyi kirbyi Denn.

The aedeagus of E. kirbyi kirbyi is a mirror image of E. k. revelierei.

- b) Pselaphus heisei heisei Herbst (Fig. 4.80 e).

P. heisei parvus Kar. (Fig. 4.80 e).

P. heisei skopljensis Kar.

There is inversion of the internal sac structures.

3. Polymorphism in male genitalia

- a) Arthromelus rivularis Jeannel

The male exists in three forms with distinct abdominal tergites and genitalia. All three varieties are found together in the same biotope (Fig. 4.81) (Jeannel, 1957).

- b) Euplectus punctatus punctatus Muls. (Fig. 4.80 b).

E. punctatus tholini Guilb.

- c) Euplectus bonvalouri narentinus Reitt. (Fig. 4.80 c)

E. bonvalouri rosae Raffr.

- d) Bryaxis curtisi curtisi (Leach) (Fig. 4.80 d)

B. curtisi orientalis (Kar.)

Fig.4.80 Inversions of the aedeagus in species of Pselaphidae (after C.Besuchet in Freude,Harde & Lohse, 1974),

- a) Euplectus kirbyi revelieri and E.k.kirbyi
- b) E.punctatus punctatus and E.p.tholini
- c) E.bonvoulori narentinus and E.b.rosae
- d) E.curtisi curtisi and E.c.orientalis
- e) Pselaphus heisei heisei and P.h.parvus

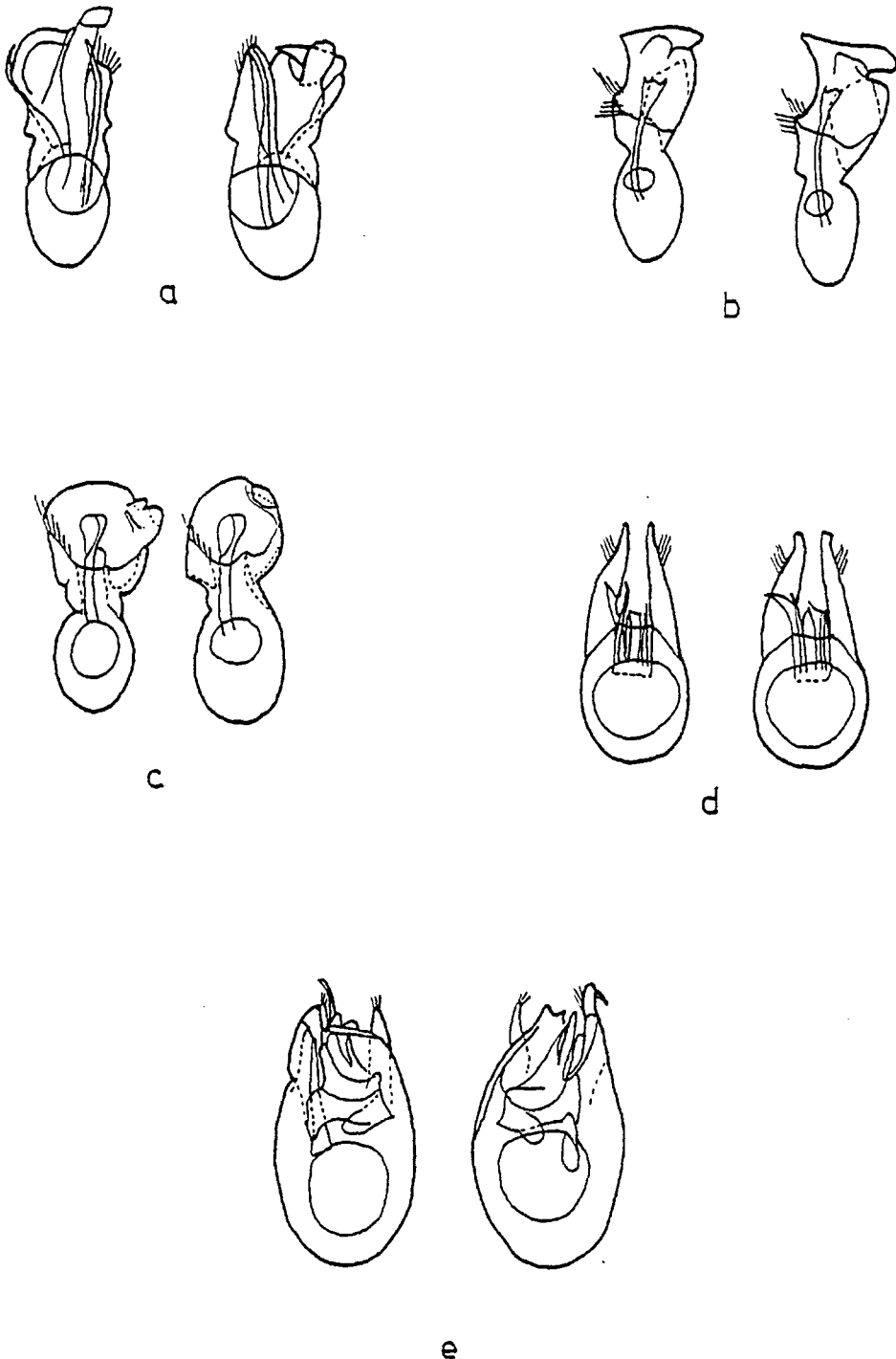
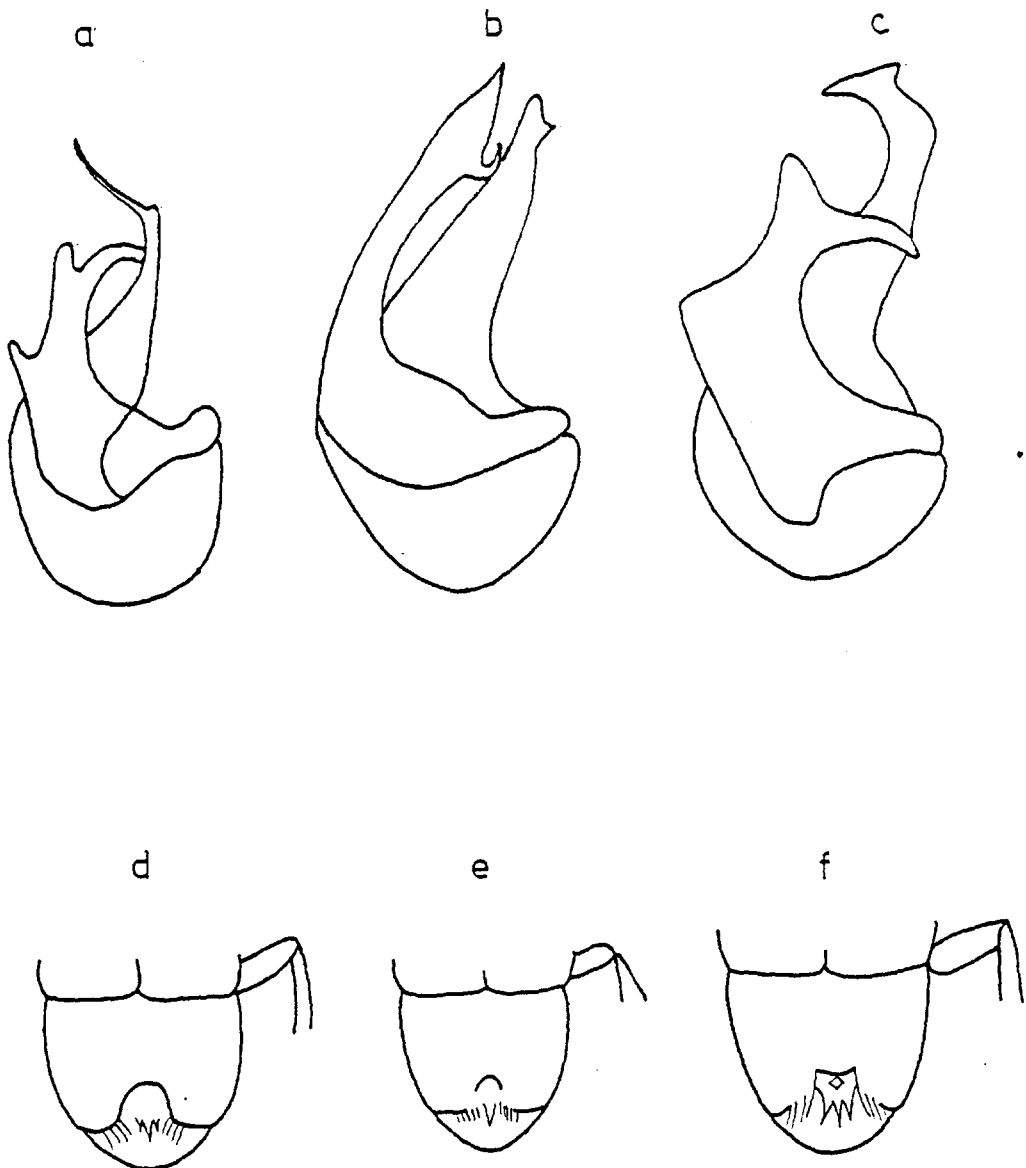


Fig.4.81 Male genitalia of Arthromelas rivularis (after Jeannel,1957)

a) var.frigilis, b) typical form, c) var.barbatus ,

Abdominal sternites of A.rivularis

d) var.frigilis, e) typical form, f) var.barbatus.



4.4 SUMMARY

A survey of the secondary sexual features in the Staphylinidae has been undertaken in order to present examples from the major subfamilies of those structures which may be involved in the production of specific tactile signals. These are contrasted with secondary sexual structures, including those from other families, which are known or suspected to fulfil other functions.

Tactile signalling during courtship may be particularly common in insects which, as adults, inhabit substrate habitats. Where environments are particularly heterogeneous and resources are patchily distributed a marked divergence in putative tactile recognition devices is common. The Staphylinidae are rich in examples of such divergent developments; a number of these are illustrated.

Conclusions are not drawn in many cases because the function of structures of this kind cannot be unequivocally established without support from other areas of research, such as mating behaviour. In the majority of the subfamilies observations on mating behaviour have not been made and little information is available regarding the biology of the species. Generally, in the past, comparisons of closely related species have not been undertaken. During the present investigations an attempt to remedy this situation in the Staphylininae has been made and morphological data is correlated with mating behaviour observations (Sections 5 & 7).

The chapter aims to present a selection of cases where features of a certain type are present, in closely related species which are known to co-exist in specific ecological situations. The hypothesis is that these features share a similar function as part of a tactile signalling system which operates after the onset of courtship behaviour.

SECTION 5

MATING BEHAVIOURIntroduction

Mating behaviour is described for the first time in a number of staphylinid species, with detailed and comparative descriptions for three apparently closely related species of Philonthus; P. cephalotes, P. parvus and P. sordidus. The three species were frequently available for collection and were cultured in constant temperature conditions: their morphology and possible relationship to one another are discussed elsewhere (Sections 4 and 7). Inter and intra-specific behaviour in P. cephalotes and P. sordidus was investigated in order to understand the implications of any differential behavioural responses in the operation of reproductive barriers between the two species.

The effect of antennectomy on mating behaviour in P. sordidus is briefly noted, since it is considered that male antennal contact with the female body is an integral part of sexual recognition by chemoreception. Antennation of the female abdomen is a necessary part of a sequence of stimuli during courtship by which the female may discriminate between con and contra-specific males.

A review of mating behaviour in the Coleoptera is collated from the literature (Source: Zoological Record 1899-1974, Entomology Abstracts - 1979) in order to show that different types of signal are produced by males and females during courtship. Some of these, which may be employed in barriers to reproduction between species, may be correlated with the general ecology of the group in question. Different types of reproductive barrier are further discussed in relation to groups in which cross-mating or hybridisation occurs in nature or under laboratory conditions.

5.1. Methods for Observation of Mating Behaviour

Observations of mating behaviour were carried out in small perspex

boxes 55 x 35 x 20 mm similar to those used for culturing (Section 2). The floor of the box was covered with dampened filter paper, onto which one male and one female were simultaneously placed.

The conditions under which observations were made varied, the most successful being the same as those in which the beetles had been cultured, 16°C and 12hr / 24 hr light regime in artificial light which on a Universal Exposure Meter, Sangamo Weston Ltd, Model S461.5, gave a reading of 8.5 on an arbitrary scale where 0= Dark, 16= Bright Sunlight.

Mating behaviour was observed in pairs of beetles which had been previously separated, one individual per box, for at least 12 hours before the mating trial. In many cases this period was longer, sometimes up to 2 weeks. From previous observations it was found that the effect of keeping the sexes separate was to increase the likelihood of mating. Nevertheless, pairs were observed to mate more than once if kept together. Observation periods were for variable lengths of time, but if copulation had not taken place within one hour the pair were again separated. Pairs were generally separated once copulation was completed.

A formal description of mating behaviour is included here only when several replications were possible. Where this is not the case, notes and observations are included.

5.2 List of Species in which Mating Behaviour Observed.

Philonthus cephalotes (Grav.), P. parvus Sharp and P. sordidus
(Grav.)

P. discoideus (Grav.) 5.2.2

P. fimetarius (Grav.) 5.2.3

P. longicornis Steph. 5.2.4

P. marginatus (Strom.) 5.2.5

P. politus (L.) 5.2.6

P. tenuicornis Muls. & Rey 5.2.7

Quedius mesomelinus Marsh. 5.2.8

Q. tristis (Grav.) 5.2.9

Rugilus orbiculatus (Payk.) 5.2.10

Othius myrmecophilus Kiesenw. 5.2.11.

Gyrohypnus fracticornis (Mull.) 5.2.12

Oxytelus sculptus Grav. 5.2.13

Tachinus signatus Grav. 5.2.14

Cypha longicornis (Payk.) 5.2.15

Tachyporus hypnorum (F.) 5.2.16

5.2.1 Philonthus cephalotes, P. parvus, and P. sordidus

1. General Description

In their studies on mating behaviour in the Meloidae, Pinto (1972a,b,c 1975, 1977), Selander (1964), and Selander and Pinto (1967), defined the characteristic positions and components of courtship and identified phases into which these may be categorised, e.g. preliminary, display, dorsal, posterior and genital phases.

A similar classification is devised here for ease of describing mating behaviour of Philonthus species. Four phases, not all of equal duration, are recognised:-

A. Precopulatory Phase

- (1) Examination of female abdominal apex by male.
- (2) Examination of male abdominal apex by female.
- (3) Prolonged examination of female by male.
- (4) Mounting by male.
- (5) Extrusion of male genitalia.

B. Copulatory Phase

Intromission.

C. Terminal Phase

D. Post Copulatory Phase

Of the four phases, the terminal phase is the least well

defined, its commencement being particularly difficult to establish.

The following description is based on observations of 165 conspecific matings. Two separate sequences of behaviour are illustrated in Plates 5.1 - 5.15.

A. Precopulatory Phase

Courtship is frequently initiated when the pair meet face to face whereupon antennal fencing occurs (Plate 5.13b). This may lead to an aggressive display where both individuals open their mandibles and make biting movements aimed at the partner's mandibles, during which the pair may fall onto their sides, their legs entwined in a venter-venter position. At the end of such a display both beetles return to their feet and the male may then move to a new position where his mouthparts are in contact with the female abdominal apex. On occasions antennal fencing and aggressive displays may be bypassed, courtship then begins at Stage(1).

(1) Examination of female abdominal apex by male

The male antennates and palpates the female abdominal apex, while the female either remains still or moves away from the male. Numerous observations demonstrate that female receptivity is indicated by standing still when being examined by the male. However, an ultimately receptive female may move away from such a male several times, before standing still when the male continues the sequence of courtship behaviour. A male usually pursues the female, if she moves away, repeating the antennation and palpation many times (Plates 5.1a, 5.14a,b).

(2) Examination of male abdominal apex by female

The female may briefly antennate and palpate the male abdominal apex during the preliminary stages of courtship, but this activity is seen comparatively rarely.

Plates 5.1a-d. Time lapse photographs of mating behaviour in Philonthus cephalotes. (5 frames/second, x 10). Sequence 1.

- a) end of prolonged examination of female by male, Stage (3).
- b) mounting of female by male, Stage (4).
- c) extrusion of male genitalia and positioning at the female genital orifice, Stage (5).
- d) insertion of the male genitalia, Stage (6).



a



b



c



d

Plates 5.2a-d. Time lapse photographs of mating behaviour in Philonthus cephalotes. (5 frames/second, x 10). Sequence 1.
a-d. insertion of the male genitalia, Stage (6).



a



b



c



d

Plates 5.3a-d. Time lapse photographs of mating behaviour in Philonthus cephalotes. (5 frames/second, x 10). Sequence 1.

- a) following incorrect insertion of the genitalia, withdrawal of the male genitalia while still in the mounted position.
- b) extrusion of the male genitalia for a second time followed by probing of the female abdominal apex.
- c-d) positioning of the male genitalia at the female genital orifice and opening of the lateral lobe.



a



b



c



d

Plates 5.4a-d. Time lapse photographs of mating behaviour in Philonthus cephalotes. (5 frames/second, x 10). Sequence 1.

a-c) positioning of the male genitalia at the female orifice and opening of the lateral lobe.

d) insertion of the male genitalia and release of grip from female.



a



b



c



d

Plates 5.5a-d. Time lapse photographs of mating behaviour in Philonthus
cephalotes. (5 frames/second, x 10). Sequence 1.
a-d) in copula.



a



b



c



d

Plates 5.6a&b. Time lapse photographs of mating behaviour in Philonthus
cephalotes. (5 frames/second, x 10). Sequence 1.
a&b) in copula.

a



b



Plates 5.7a&b. Time lapse photographs of mating behaviour in Philonthus
cephalotes. (5 frames/second, x 10). Sequence 1.
a&b) in copula.

a

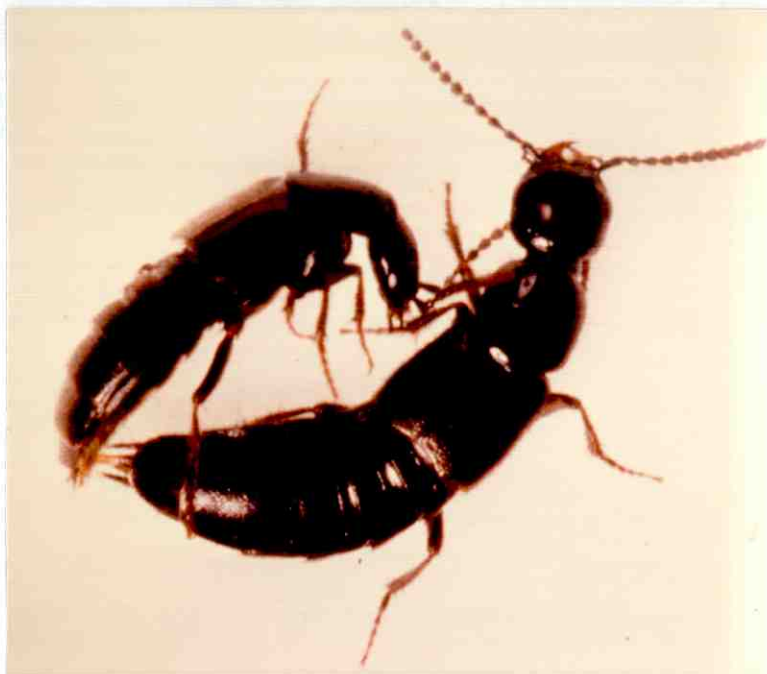


b



Plates 5.8a&b. Time lapse photographs of mating behaviour in Philonthus
cephalotes. (5 frames/second, x 10). Sequence 1.
a&b) in copula.

a



b



. Plates 5.9a&b. Time lapse photographs of mating behaviour in Philonthus cephalotes. (5 frames/second, x 10). Sequence 1.

a) female begins to move during ~~int~~romission.

b) female starts to walk away during intromission.

a



b



Plates 5.10a&b. Time lapse photographs of mating behaviour in Philonthus cephalotes. (5 frames/second, x 10). Sequence 1.

a) female restless during intromission.

b) female turns her head towards the male and makes antennal contact.

a



b



Plates 5.11a&b. Time lapse photographs of mating behaviour in Philonthus
cephalotes. (5 frames/second, x 10). Sequence 1.

a) female moves away from the male.

b) intromission ends.

a



b



Plates 5.12a&b. Time lapse photographs of mating behaviour in Philonthus
cephalotes. (5 frames/second, x 10). Sequence 2, Approach
Phase only.

a&b) male antennal fencing over female.

a



b

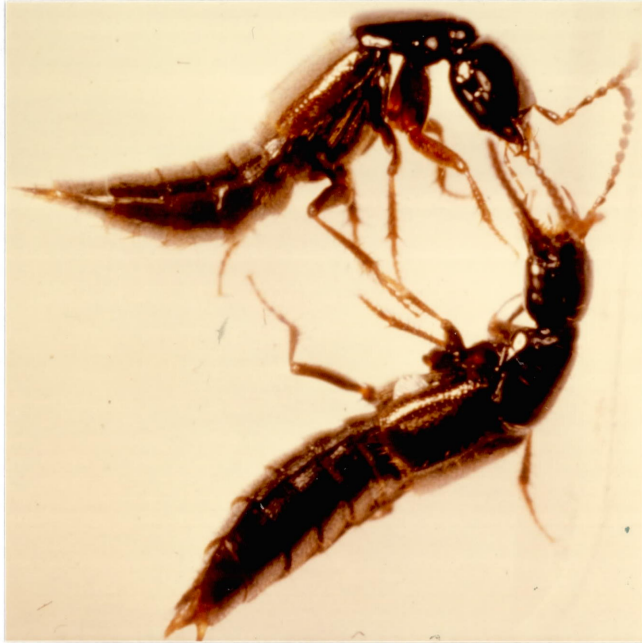


Plates 5.13a&b. Time lapse photographs of mating behaviour in Philonthus
cephalotes. (5 frames/second, x 10). Sequence 2, Approach
Phase only.
a&b) face to face anternal fencing.

a



b



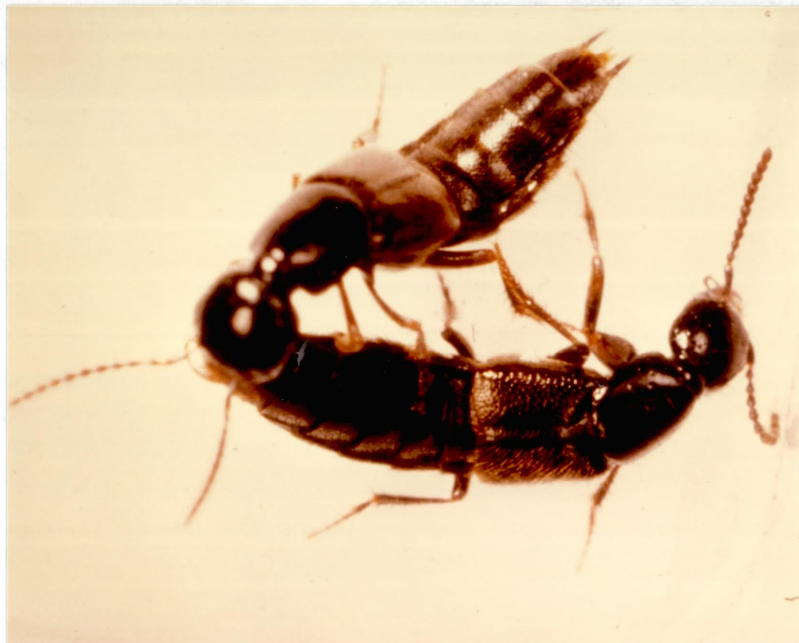
Plates 5.14a&b. Time lapse photographs of mating behaviour in Philonthus cephalotes (5 frames/second, x 10). Sequence 2, Approach Phase only.

a&b) male moves to the female abdominal apex for it's examination, Stages (1) and (3).

a



b



Plates 5.15a-c. Time lapse photographs of mating behaviour in Philonthus cephalotes. (5 frames/second, x 10). Sequence 2; Approach Phase only.

a) mounting of female by male.

b&c) extrusion of male genitalia.

a



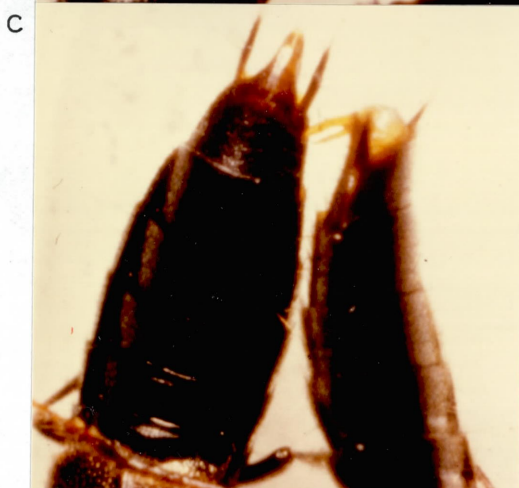
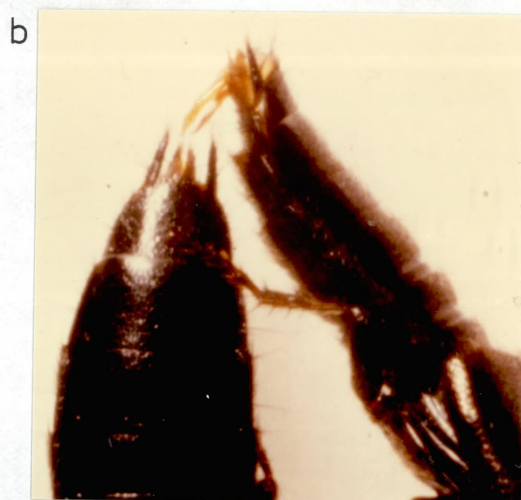
b



c



Plate 5.16a - h. Photographs to show the probing of the female abdominal apex by the male genitalia, separation of the lateral and median lobes of the male genitalia, and entry into the female genital orifice during mating of Philonthus cephalotes. Photographs are not in sequence.



(3) Prolonged examination of female by male

If the female remains still during the initial examination of her abdominal apex by the male, this activity is prolonged and developed to include antennation and palpation of the dorsal and ventral abdominal surfaces, often assisted by the female slowly moving her abdomen up and down. The female may remain still or move away from the male, thereby interrupting the courtship sequence.

(4) Mounting by male

If the female remains still during (3) the male continues to antennate and palpate the abdomen and begins to move anteriorly over the dorsal surface of the abdomen at the same time rubbing against the sides with the tibiae of the pro and meso-thoracic legs (Plates 5.1b & 5.15a). While moving forward the male antennates, in turn, the female elytra, pronotum and head. The sequence may be interrupted at this stage if the female moves away from the male.

(5) Extrusion of male genitalia

Following mounting, (4), if the female remains still, the male takes up a new position to one side of the female, (more often the left side), and the pro-thoracic legs rub the dorsal and ventral surfaces of the anterior abdomen while the meso-thoracic legs rub the dorsal and ventral surfaces of the apex. The male genitalia are extruded, and the apex of the median lobe is probed around the female abdominal apex and genital orifice (Plates 5.1c & d, 5.2, 5.3, 5.4a, b & c, 5.15b & c, 5.16a-h). The genitalia may be probed around the female genital orifice for several seconds, or the genitalia may be withdrawn and extruded several times prior to insertion. If the female is not receptive she curls her abdominal apex ventrally, which is likely

to effectively impede insertion of the male genitalia, and she kicks the male abdominal apex with her meta-thoracic legs. The meso-thoracic legs are often kicked up and down at the same time. More aggressive behaviour is observed in some females which rapidly move the abdomen up and down, and turn to face the male with the mandibles open, biting at the males head and legs.

B. Copulatory Phase

Intromission

Following extrusion of the male genitalia, (5), the apex of the median lobe is inserted into the female genital orifice. After insertion, and presumably when the internal sac is evaginated, the male ceases antennation, palpation and leg rubbing and remains in the position to one side of the female. During this the male is supported on the legs ventral to the female, while those dorsal to the female rest on the female dorsum or are held just above. The male does not grip the female at this stage (Plates 5.5, 5.6, 5.7 & 5.8) although the dorsal meta-thoracic leg may rest on the genital connection.

During intromission the female remains still, grooms, or may eat if food is present. If the female becomes active the male may stroke or tap her dorsum with the antenna or legs on the dorsal side. The female may walk around during intromission as a consequence of which the male is forced into an end to end position, in which he is dragged behind the female. When this occurs the male either rests on his dorsal side or walks backwards behind the female (Plates 5.9, 5.10d & 5.11a). The male position, to one side of the female, may be resumed if the female becomes still again. Frequently, an active female was observed to become still after a male had tapped vigorously on her dorsum with his pro-or meso-thoracic legs.

Abdominal movement during intromission generally is slight, there may be lateral movement of the valvulae of the female ninth abdominal segment and some telescoping of the ninth into the eighth abdominal

segment. Nothing of this kind has been observed in the male (Plate 5.11b).

C. Terminal Phase

The terminal phase cannot easily be defined since retraction of the male genitalia is not triggered by any observable event. However, the female becomes slightly more active just prior to retraction and alternate lateral movement of the valvulae of the ninth abdominal segment, with slight dorso-ventral expansion of the genital segment are frequently observed. A pumping movement within the median lobe has been observed at this time and some males moved their legs and antennae, whilst placing a meta-thoracic leg on the genital connection just before the genitalia were withdrawn.

D. Postcopulatory Phase

After retraction of the genitalia the pair generally move away from each other and remain still for a few seconds while both beetles move the valvulae of the ninth abdominal segment laterally and alternately towards the mid-line. This may be the initiation of the grooming behaviour which usually follows. In general there is no physical contact between the pair for several minutes following copulation.

2. Comparative description of mating behaviour in Philonthus cephalotes, P. parvus and P. sordidus.

Following observation of many pairs of the three closely related species of Philonthus, which can be found syntopically in synanthropic habitats, observable differences in courtship behaviour are found to be small.

During the terminal phase P. sordidus retracts the genitalia immediately into the abdomen and moves away from the female, whereas in P. parvus, the male may rest the median lobe beside the female genital orifice for a few seconds before retraction of the genitalia into the abdomen; the pair then move apart. Further observations

should be made to confirm whether this is a constant feature of post copulatory behaviour.

The duration of copulation, timed from the start of intromission, differs considerably in the three species:

<u>P. cephalotes</u>	1m 25.5s - 1m 54s (n = 9)	= 1.65m $\pm$ 0.041
<u>P. parvus</u>	35 secs - 4 mins (n = 13)	= 2.173m $\pm$ 0.301
<u>P. sordidus</u>	20 mins - 80 mins (n = 8)	= 44.625m $\pm$ 6.903

P. parvus males have been observed to mate several times in quick succession: in these cases after copulation the male does not leave the female and continues to antennate and palpate her pronotum, elytra and head following which the courtship sequence begins again. This occurred more frequently if the male had been kept separately from females for some considerable time (i.e. several days). P. cephalotes males also mate several times in succession; up to three matings in one hour have been recorded (Section 5.3). P. sordidus have not been seen to mate more than once during observation periods of up to two hours.

Differences may occur in the duration of individual components of the courtship sequence. This has not been investigated here, although it is suspected that any such differences would be small.

Intra and inter-specific behaviour in P. cephalotes and P. sordidus is investigated in Section 5.3. The effect of antennectomy of male P. sordidus is discussed in Section 5.4.

5.2.2 Philonthus discoideus

Three pairs observed from a 20°C and 16hr/24hr artificial light regime.

One male and two females were placed together and immediately the male mounted, in turn, both of the females. Before and during mounting the male palpated and antennated the dorsal and ventral abdominal surfaces of the female. When mounted the male is dorsal to the female (facing the same direction) and his maxillary palps rest on the dorsal surface of the abdomen, just posterior to the apex of the elytra. The male arched his abdomen so that the genital orifices of the two sexes were opposed. The male, however, did not extrude the genitalia when mounting either of the two females and dismounted after a short pause. Following this the male only mounted a female after an aggressive display which consisted either of:-

- a) face to face, mandible to mandible biting and antennal fencing which lead to an entangled leg struggle in the venter to venter position, or
- b) approach of the male from behind the female, touching the apex of her abdomen with his antennae or mouth parts. Following this the female turned around to face the male. This lead onto an entangled leg struggle as above (a).

During and after these aggressive encounters the male attempted to attain the copulatory position, which is notably different to the other observed Philonthus species since the position of the male head is more posterior. Successful intromission depends on the female remaining still. Intromission, lasting only a few seconds, was observed before the pair were disturbed by the second female.

General Observations

Unlike P. cephalotes, P. parvus and P. sordidus, approach and

mounting of the female was carried out very rapidly with little preliminary courtship behaviour. It is also notable that the male does not rub the fore and mid legs against the sides of the female abdomen during mounting as in P. cephalotes, P. parvus, and P. sordidus. Instead, while in the copulatory position, the P. discoideus male strikes the sides of the female abdomen with all three pairs of legs.

Investigations were carried out to determine whether a male, in which courtship behaviour but not copulation had been observed, would exhibit the same behaviour towards the same female anaesthetised by CO₂. Copulation had not been achieved because the female exhibited her non-receptivity by curling her abdomen ventrally during the mating attempt. The male did not exhibit courtship behaviour towards the immobilised female. Further observations of this type are required before any conclusions can be drawn.

5.2.3 Philonthus fimetarius

One pair observed from a 20°C and 16hr/24hr artificial light regime.

Males and females only appeared to be aware of each others presence after antennal contact had been made. Some aggressive behaviour was observed, the male biting the female abdominal apex, and antennal fencing but no courtship behaviour was exhibited.

5.2.4 Philonthus longicornis

One pair observed from a 16°C and 12hr/24hr light regime at 16°C, 20°C and 23°C.

Immediately upon being placed together the male ran very quickly to the female and mounted her dorsum. During mounting the male head was held downwards and the maxillary palps touched the female abdomen. The genitalia were extruded and inserted into the female, and

intromission lasted about 15 seconds after which the male dismounted and moved away from the female.

After several minutes the male mounted the female again and both remained still in the copulatory position for a few seconds. The male then dismounted without extruding the genitalia. A few minutes later intromission took place for a second time and lasted approximately 5 seconds.

On the following day the same pair were placed together again. The same behaviour was repeated with the male immediately running onto the female dorsum and culminating in intromission which lasted a few seconds.

Precopulatory behaviour, found in other Philonthus species, including antennation and palpation of the female abdominal apex, did not occur.

5.2.5 Philonthus marginatus

One pair observed from a 16°C and 12hr/24hr artificial light regime.

When a male and female were placed together, the male immediately mounted the female by climbing anteriorly over her dorsum until his maxillary palps and antennae were in contact with those of the female. The male then dismounted and the female remained still. After a few seconds the male remounted into the same position and immediately extruded and inserted the genitalia into the female without further palpal or antennal contact. Intromission followed in the usual Philonthus position, with the male to one side of the female. Intromission lasted approximately 45 seconds. The male reattained a position dorsal to the female and, whilst gripping her with the fore and hind legs, the genitalia were withdrawn. The male then remained in this position for 30 seconds following copulation before dismounting

and moving away from the female.

A few minutes later the male mounted the female again whilst beating his antennae vigorously over her dorsum. The genitalia were inserted and the male turned clockwise into an end to end position with the female. Both sexes remained still during the second intromission which lasted 20 seconds. The male dismounted immediately following intromission.

After a brief separation, the male began again to pursue the female touching the apex of her abdomen with his maxillary palps and antennae. 5 minutes later intromission took place for a third time. On this occasion the male palpated and antennated the female head upon mounting and then moved posteriorly into the copulatory position where the genitalia were extruded and inserted into the female. The male assumed a position to one side of the female and intromission was terminated only 3-4 seconds later. On a separate occasion intromission in the same pair lasted for 90 seconds.

The observation and culture boxes containing P. marginatus emitted a characteristic odour, possibly due to pheromones, which may be utilised during mating. This was not investigated further.

5.2.6 Philonthus politus

Seven pairs observed from a 16°C and 12hr/24hr, artificial light regime.

Mating behaviour is very similar to that described for Philonthus cephalotes, P. parvus, and P. sordidus. On placing a male and female together in an observation box, they did not appear to detect one another until physical contact was made, at which time the male immediately mounted the female, climbing forward over her dorsum from one side until his head became level with the female pronotum. Mounting was usually preceded by very brief antennation and palpation

of the female abdominal apex as in P. cephalotes, P. parvus, and P. sordidus. The male then moved the ventral surface of his abdomen over the dorsal surface of that of the female. The male adopted a position to one side of the female where the genitalia were extruded and inserted into the female genital orifice. During intromission the male remained in the position to one side of the female, released his grip on her, then dismounted immediately the genitalia were withdrawn and moved away from her. The duration of intromission did not exceed 10 seconds.

Twenty minutes later one of the pairs mated a second time, and as before it was of a few seconds duration.

General Observations

Aggressive behaviour has also been observed in P. politus. The male may quickly approach a female with his mandibles open wide, either directed towards the female's head or her abdominal apex. In response the female may sharply raise her abdomen several times in the direction of the male. Often the female remained still with her abdomen raised, during which time the male antennated and palpated the ventral and dorsal surfaces, and mounted in a position in which his head became level with her pronotum. Both beetles remained still in this position for a few seconds, the male not extruding the genitalia, the male then dismounted and walked away from the female.

Face to face encounters often ended in a venter to venter "struggle" where the legs of the pair became entangled.

Inter-specific Behaviour

A female P. tenuicornis and female P. politus were put together into an observation box. The two species are fairly closely related, P. tenuicornis being slightly smaller. To this pair a male P. politus was then introduced. The male approached, briefly antennated,

palpated and copulated immediately with the female P. politus.

The male behaviour was extremely aggressive towards the female P. tenuicornis. Thereafter each time the male came upon the female P. politus, he antennated and palpated her dorsum. The male seemed able to recognise the female of the other species before any contact was made between them and initiated aggressive displays towards her.

Following this a new female P. politus, introduced to the same box, briefly touched the apex of the male abdominal apex with her antennae and maxillary palps. The male immediately mounted, touching the female abdominal tergites with his maxillary palps as he climbed forward, and mated with the new female. Intromission, lasted about 7 seconds.

5.2.7 Philonthus tenuicornis

One pair observed from a 20°C and 16hr/24hr artificial light regime.

The male and female were placed together and during the first 20 minutes only aggressive displays were observed. On three occasions following this the female abdominal apex was antennated and palpated by the male, in a similar way to that found in P. discoideus, before mounting. The male, however, did not extrude the genitalia. The female remained restless while being mounted by the male, an indication of non-receptivity.

5.2.8 Quedius mesomelinus

General Observations

Observations were made on pairs which had been collected as larvae and reared in the laboratory (Section 6). 14 to 16 days after emergence of the adults, virgin males and females were placed together in pairs and their behaviour observed.

Numerous observations were made during this period with different

combinations of pairs but in all cases the same type of behaviour was observed. Once the pair were placed together both were very active, running around the observation cage. Physical contact was made between the pair, most frequently by the male opening his mandibles wide and gripping the female abdominal apex. Following this the male either released his grip on the female and moved away, or the female turned to face the male after which an aggressive display followed in which the legs of the pair became entwined. After such physical contact the female alone, or both the male and female together, displayed "abdomen wagging". This was the rapid movement up, down and from side to side of the abdominal apex which was directed towards the other individual. The female turned so that her abdomen was directed towards the male head. When both the male and female displayed synchronous abdominal wagging the pair faced away from each other, often at 90-180°, while the apices of their abdomens remained in contact. Both abdomens were wagged up and down almost in synchrony while making contact on each downstroke. During this period the male did exhibit some antennation and brief rubbing of the fore and mid legs on the female abdominal apex (similar to Philonthus sordidus mating behaviour). However, on each occasion the female did not remain still and frequently exhibited abdomen wagging.

During this time the behaviour of pairs of males and pairs of females was compared with intersexual behaviour. Male to male behaviour was very aggressive. Antennal contact was frequently followed by gripping the abdominal apex of the other beetle with the mandibles, displays in which the legs of both individuals became entwined, and abdomen wagging as described above. One individual would often run towards the other from a distance of 2-3 cm with the mandibles open. Female to female behaviour was less aggressive but

with some abdomen wagging. Hence at this stage of development there was little difference between intersexual and intrasexual behaviour.

On the eighteenth day after the first adults emerged all the virgin beetles were transferred to a 20°C and 16hr/24hr artificial light regime and the effect of this on the behaviour between potential mates was monitored over the following two months. During this time similar behaviour was again observed and although some preliminary courtship behaviour was exhibited by the male, aggressive displays (mandible-abdominal apex) and abdomen wagging were predominant.

Description of mating behaviour of mature adults

Numerous observations at 21-24.5°C from a 16hr/24hr artificial light regime.

Upon placing a pair together in an observation box, physical contact was made after a short space of time. This consisted either of face to face antennation, where the male took the female antennae alternately between his mandibles, or of antennation of the entire body of the female with the male in a position to one side of the female. Abdominal wagging was often observed at this time, as well as biting of the female abdominal apex. Following abdomen wagging the male turned to face the female abdominal apex and proceeded to antennate it. On one occasion a male was seen to approach a female from the side, grip the pronotum with the mandibles and legs and then climb onto the female dorsum into the mating position in which the male faces the same direction as the female. The male sometimes also mounted the female from the head, climbed posteriorly onto her until his head was level with the elytra and then turn 180° into the normal mating position. In general, mounting followed antennation and fore-leg rubbing of the female abdominal apex, during which time

the male climbed anteriorly over the female dorsum until his head was level with the pronotum. Prior to extrusion of the genitalia the male abdominal apex was often rubbed over the female tergites from side to side. The genitalia were then extruded and rubbed from side to side over the female ninth tergite and inserted into the female genital orifice. As soon as insertion was complete the male moved to an end to end position with the female. During intromission the antennae of both individuals remained still. Pulsations of the abdominal apices in an antero-posterior direction and lateral movements of the valvulae were carried out for extensive periods, the frequency of the pulsations increasing intermittantly. Periodically the female turned to face the male abdominal apex with open mandibles, during intromission, and then returned to her former position. The male moved from the end to end position to come along side the female. Just prior to termination of intromission the pulsations of the abdomens receded and the genitalia were withdrawn. The duration of intromission varied between 12 seconds and 64 minutes in 6 pairs. This variability may be accounted for by the laboratory conditions. Following copulation the pair moved away from each other then often a few seconds later the male returned to the female and rested his antennae or mouthparts on the female elytra or abdominal apex. Reactions between the pair following this were frequently aggressive.

During the sequence of courtship behaviour termination may occur at any time, depending on the receptivity of the female. An unreceptive female did not remain still during courtship and either turned towards the male and opened her mandibles, or rapidly raised her abdomen in the air.

The first matings were observed between virgin pairs 4 months after adult emergence. Mating was continually observed over the following 3 months. It is likely that the laboratory conditions

contributed to this. Little is known of the biology of Quedius mesomelinus in the field and it is not known whether this extended mating period is natural.

5.2.9 Quedius tristis

Two pairs were observed from a 20°C and 16hr/24hr artificial light regime.

Preliminary courtship behaviour and mounting was observed in a pair in which intromission did not take place. The male approached the female very slowly and cautiously from a posterior position, with his antennae held horizontal and directed anteriorly. Occasionally one or both fore legs were raised and held in the air. The approach of the female towards the male was similarly cautious, perhaps because of the aggressive behaviour observed when the pair had previously met face to face. When the female approached the male she opened her mandibles and nipped the male's abdominal apex. If the male turned to face the female during an approach of this kind, both sexes opened their mandibles and, in the face to face position, nipped each other.

After one hour together the male, on two occasions, positioned himself just posterior to the female abdominal apex. This occurred after the male had approached the female face to face, both sexes with their antennae outstretched and mandibles open. Just before face to face contact was made the male moved to the posterior position, which in other pairs preceded mounting, nevertheless mounting did not occur.

In a second pair the beginning of courtship was not observed, but observations began when the pair were in copula in the end to end position. The male abdominal apex exhibited rapid pumping movements at the start of intromission. Pumping then continued more slowly throughout intromission. The time from the beginning of observations to the termination of intromission was 31 minutes.

5.2.10 Rugilus orbiculatus

Two pairs observed from a 20°C 16hr/24hr artificial light regime.

Observations began just prior to mounting. The male gripped the female around her neck with his open mandibles, facing in the same direction as the female, and then climbed onto the female dorsum gripping her abdomen with his legs. In the mounted position the male proceeded to rub the sides and ventral surface of the female abdomen with the hind legs. At the same time, the female curved her abdominal apex dorsally while the male arched his abdomen, so that the apex passed over that of the female, bringing the ventral surfaces of both abdomens together at their apices. After a few seconds the male genitalia were extruded and the apex of the median lobe moved towards the female genital orifice. The male genitalia were inserted into the female and both beetles remained still, the male with his hind legs gripping the apex of the female abdomen.

Just prior to termination of intromission, the female began to move her legs and walked around. The male then withdrew the genitalia, retracting the median lobe immediately into the abdomen. The male removed his mandibles from around the females neck, dismounted and the pair separated.

The duration of copulation was approximately $2\frac{1}{2}$ minutes.

The pairs which had been observed in copula were collected on 27.2.77, mating was seen a few days later. Larvae conforming to a description of 1st instar Rugilus orbiculatus by Kasule (1970) resulting from these pairs were observed on 9.5.77.

5.2.11 Othius myrmecophilus

A single pair observed on two occasions, 1. in the field, 2. at 22°C, from an 18°C, 16hr/24hr artificial light regime.

In the field a single male and female were collected in separate deep litter samples. When inhaled into the same pooter the male immediately mounted the female. It was not ascertained whether intromission occurred. Details were confirmed under laboratory conditions.

The pair were placed together in an observation box. The male immediately began to pursue the female, his head approximately 1-2cm away from the female abdominal apex. After about 2 minutes the male came closer to the female and rapidly climbed forward over her dorsum placing his open mandibles around her neck. At the same time the male antennated the females head. In the mounted position the male gripped the female, his fore and mid legs around the sides of the pronotum and the hind legs around the sides of the abdomen. The male then arched his abdomen bringing the everted internal sac into alignment with the female genital orifice. Following this the male withdrew the internal sac from the female after only a few seconds. The pair separated and moved away from each other but after a few seconds the male again mounted the female, and while in this position the male everted the internal sac which was then rubbed over the terminal tergites of the ventrally curved female abdomen. The female then curved her abdominal apex dorsally, the male arched his abdomen and the internal sac was inserted into the female genital orifice. The internal sac was withdrawn after only 20 seconds. After disengagement the male remained in the mounted position and inserted the internal sac into the female 3 further times but each time intromission lasted only a few seconds. During this behaviour the male antennae were directed vertically while those of the female were beating rapidly. The male inserted the genitalia again and after 1m. 24 secs., moved into an end to end position

where both beetles groomed intermittently. Initially in this position the female occasionally walked around, the male being forced to walk backwards behind her, but for most of the time in copula the pair remained still. Just prior to termination of intromission the female began to walk around, dragging the male behind her. Following this the male arched his abdomen slightly to pull on the female from the last abdominal segment. At the same time the male turned around to face the same direction as the female and touched the female abdomen with his mandibles. The female then walked on again forcing the male back into the end to end position. Again the male pulled on the female abdominal apex turning round at the same time, and the internal sac was withdrawn after 48½ minutes in copula.

Following mating the pair moved away from each other.

5.2.12 Gyrophypnus fracticornis

Two cages, each with one male and three females were observed at 22°C from an 18°C and 16hr/24hr artificial light regime.

Both boxes were observed for one hour and during this time each male antennated and palpated the abdominal apex of each female. The males and females were then separated for one hour after which time they were placed together again. On this occasion the males immediately began to pursue each of the females in turn. Five different sequences of courtship behaviour were observed:

- 1) antennal fencing for about 30 seconds before separating without further contact.
- 2) antennal fencing, the male then turning to face the female abdominal apex after which mounting occurred.
- 3) antennation of the female abdominal apex by the male, particularly the long setae which protrude laterally, meanwhile palpating

and touching the female dorsum with his mandibles. The male then repeatedly curled his abdomen ventrally and slightly to one side. At the same time all three legs on one side were lifted and the abdominal apex was brought well forward. The sclerites around the ventral genital orifice were opened and aligned with that of the female. During this behaviour the male continued to antennate the female abdominal apex. This behaviour was repeated several times with each of the females but was not carried through to intromission. The male seemed unable to align the genital openings and each female walked away while sharply raising her abdomen. It is necessary that the female should remain still if she is receptive since the male does not grip her in any way while inserting the internal sac.

4) The male palpated and antennated the dorsal surface of the female with his head level with her pronotum, elytra or abdomen base. The male then subsequently moved posteriorly to the abdominal apex to begin the alignment of the abdomens as in 3).

5) after face to face antennal fencing the female curled her abdomen ventrally bringing it forwards in a similar way to that described for the male in 3). The female presented her abdominal apex to the male mouthparts. The male palpated and antennated the female abdominal apex and then curled his abdomen ventrally and brought it forwards to meet that of the female. The two abdominal apices were then rubbed together for a few seconds after which intromission occurred. The pair then assumed an end to end position until the termination of intromission. Copulation lasted 20 seconds.

5.2.13 Oxytelus sculptus

Four pairs observed at 21°C and 28°C from an 18°C and 16hr/24hr artificial light regime.

As the male approached the female he raised his abdominal apex. When in contact with the female abdomen the male antennated and palpated the apex. The female terminated this behaviour on several occasions by walking away and the male did not pursue her. Although a second female was concealed in a fold of filter paper it appeared that the male could detect her. The male began searching behaviour, his palps close to the ground and his antennae beating from side to side. Upon finding the female the male palpated and antennated her abdominal apex and climbed forwards onto her dorsum, still continuing this behaviour. The male then extruded the genitalia and inserted the median lobe into the female genital orifice. After a few seconds the male turned anticlockwise into an end to end position in which the pair remained until the end of intromission. During intromission the female was relatively still but occasionally groomed her antennae. The male, however, was very active and repeatedly opened and closed his mandibles and vibrated the maxillary palps on the substrate. The antennae were waved alternately and the mid and hind legs were frequently moved up and down.

Just prior to the termination of intromission the female became active and walked rapidly around dragging the male behind her on his dorsum. During this the male attempted to right himself by curling around and raising his head. When this was achieved the male gripped the substrate and stopped the female dragging him along but since the female was larger than the male this was not often successful. The male, however, did remount the female several times but did not grip her with his legs. The duration of intromission ($n = 1$) was 12 minutes. After termination both beetles remained still.

5.2.14 Tachinus signatus

Several pairs were observed although copulation was only seen on one occasion. Observations were carried out at 26°C from an 18°C and 16hr/24hr artificial light regime.

The male approached and palpated and antennated the female dorsum. The male then climbed onto the female pronotum from the side and turned lengthwise so that his head was at the female abdominal apex. The male palpated and antennated this area. While still mounted on the female the male turned 180° into the copulatory position. The genitalia were extruded and inserted into the female then the median lobe moved irregularly a little way in and out of the female genital orifice. There were no movements of the legs or palps by either sex throughout intromission, although the male adjusted his position slightly each time the aedeagus moved back and forth. Intromission lasted approximately 3 minutes.

After copulation the pair separated and remained still for a few seconds, then the male ran to and from the female each time brushing the ventral surface of the abdominal apex over the dorsal surface of that of the female. Intromission did not occur a second time.

General Observations

Clear observation of the function of the peg setae on the male abdominal sternites was not achieved, but during copulation they touch the female's eighth abdominal tergite.

5.2.15 Cypha longicornis

One pair observed.

Approach and mounting were not observed. In the copulatory position the male is dorsal to the female with his mouth parts touching the base of the pronotum. The male fore legs grip the

side of the pronotum base, whilst mid legs grip the side of the abdomen and the hind legs rest on the substrate behind the pair. The antennae of both male and female are held horizontal and slightly posteriorly. Occasionally the male stroked the female with the fore legs. Pulsations of the male genitalia were observed.

On being disturbed, by vibration of the observation box, the male turned to an end to end position with the female, then moved around to remount the female. The female raised her abdomen so that remounting was not possible. Disengagement of the genitalia and separation followed.

General Observations

The position taken up by Cypha during mating is atypical for the subfamily Aleocharinae, generally the male abdomen is raised up over his head prior to and during coupling. From a consideration of what is known of mating behaviour in the Aleocharinae (Section 5.5) and of phylogenetic relationships in this group (Seevers, 1978), it would seem likely that the mating position exhibited by Cypha represents a secondary development in the subfamily. The shape of the abdomen in Cypha may well be a contributing factor to this mode of coupling.

5.3 Intra and inter-specific behaviour in Philonthus cephalotes and P. sordidus

Philonthus sordidus and P. cephalotes, a pair of closely related sympatric species, can regularly be found living together in the same habitat e.g. compost heaps.

Morphologically the two species are very similar, their differences are discussed in detail in Sections 4 and 7. The most substantial differences occur in the genitalia (Figs. 7.2c&m, 7.3b, 7.4b, 7.5c, 7.6e).

Since the two species live in such close proximity the aim of the present investigation was to observe intra and inter-specific reproductive behaviour in order to understand the differential behavioural responses by which interspecific mating is avoided.

Method

For methods of observation of mating behaviour see Sections 2.2 and 5.1.

All the beetles used in the present experiments were collected as adults on the same occasion from a compost heap consisting predominantly of old grass cuttings in Sussex, England in early November 1978.

The adults were identified and cultured (Section 2.2) and allowed to settle before observations were carried out from November 1978 to February 1979. Males and females were kept singly prior to, and between behavioural observations of pairs. Each observation was undertaken with a different pair of beetles under the conditions in which they were cultured (16°C, and 12 hr/24 hr light regime) between 11.00 hrs - 17.00 hrs.

Observations were divided into four categories:-

Intra-specific Behaviour

1. ♂ P. cephalotes x ♀ P. cephalotes
2. ♂ P. sordidus x ♀ P. sordidus

Inter-specific Behaviour

3. ♂ P. cephalotes x ♀ P. sordidus

4. ♂ P. sordidus x ♀ P. cephalotes

One continuous set of observations on one pair of beetles, i.e. one trial, lasted one hour. In each category, 20 replicate trials with a different pair of beetles were carried out.

From previous observations of intra-specific mating behaviour (Section 5.2), 10 behavioural components of the courtship process have been identified and chosen for the basis of the present quantitative study. These are detailed below.

Within a one hour trial, the total number of times a particular behavioural component occurred was recorded. No attempt was made to time the components in sequence: this may provide scope for further work.

Behavioural Components. (For details refer to Section 5.21)(1) Examination of female abdominal apex by male

The male vigorously antennates and palpates the abdominal apex of the female (Plate 5.14a).

(2) Examination of male abdominal apex by female

The same activity as described in (1) with reversal of sexes. This activity is comparatively rare.

(3) Prolonged examination of female by male

If the female exhibits receptivity by standing still during the activities of (1), the behaviour carried out by the male in (1) is prolonged and developed to include examination of the entire dorsal, and sometimes ventral, surface of the female abdomen. This is often assisted by the female raising her abdominal apex slightly (Plates 5.14a & b)

(4) Mounting by male

This is always preceded by (1) and (3).

The male climbs forward onto the female abdomen, while continuing to antennate and palpate the dorsal surface and rubbing the pro and

meso-thoracic legs against the sides of the female abdomen (Plates 5.1b & 5.15a).

(5) Extrusion of male genitalia

This is always preceded by (1), (3) and (4).

Once mounting is achieved and the female is standing still, the male adopts a new position to one side of the female. The male continues to antennate and palpate the female abdomen and thorax. The male legs rub the dorsal and ventral surfaces of the female abdomen from the new side position. During this activity, the male extrudes the genitalia (once or several times) and probes the apex of the median lobe around the female abdominal apex and genital orifice (Plates 5.1c, 5.3b & c, 5.15b & c). (Each time the genitalia are extruded is counted as a single event).

(6) Intromission

Following (5), the male inserts the apex of the median lobe into the female genital orifice, ceases antennation, palpation and leg rubbing and remains still, to one side of the female. Following this the male may assume an end to end position attached only to the female by the genitalia (Plates 5.5-5.11).

(7) Aggression by female

(8) Aggression by male

Aggression is displayed when the male or female opens the mandibles wide and actively "bites" the other. The abdominal apex, legs or the mouthparts may be "bitten", the latter usually evokes a similar activity in the other beetle, whereupon the pair face each other, mandibles wide apart, and "bite" each other. An entire sequence of aggression was recorded as one single event.

(9) Avoidance by female

(10) Avoidance by male

An avoidance reaction may be displayed. This is composed of one

of the pair approaching the other face to face, stopping a few millimetres away and then after a very short pause rapidly running in the opposite direction without having made physical contact.

Components (1), (3), (4), (5), and (6) are a sequence of events. If one stage does not follow onto the next, the entire sequence must begin again.

Components (2), (7), (8), (9) and (10) are alternative events which occur in isolation; (7) and (8) may interrupt the above sequence.

Results

The results are presented in Tables 5.1-5.5.

Discussion of Results

5.3.1 General Observations

A preliminary to all further sexual behaviour between a male and female upon placing them together, in an observation box, is often reciprocal antennal contact in the face to face position (Plates 5.12 & 5.13). This is often followed by closer contact with the maxillary palpi. The behaviour which follows is a consequence of the information gained through this preliminary encounter. The occurrence of the preliminary behaviour is not recorded or further discussed.

The duration of maturation, and the times and seasons when mating occurs in P. sordidus and P. cephalotes may be different. However, there was no obvious difference in behaviour, which may be related to this, over the period of observation. With regard to this, it must be borne in mind that the object of the investigation was to compare inter-specific behaviour with intra-specific behaviour and a direct comparison of intra-specific behaviour in P. sordidus with P. cephalotes is not made here (Section 5.21).

The results are likely to be dependant to some extent on the number of encounters the pair of beetles make with each other during a trial. This in turn is probably dependant on activity levels

during the 24 hour cycle. An index of activity would be of future use, but here the problem is largely solved by a suitable number of replicate trials. Nothing is known from the literature of the periodicity of activity.

Intra-specific Behaviour

1. ♂ P. cephalotes x ♀ P. cephalotes (Table 5.1)

In 90% of the trials, after preliminary behaviour (Section 5.31), the male proceeded to examine the female abdominal apex (1) (Plate 5.14a). Except in the case of two of these males (trials 9 & 11) (1) lead onto prolonged examination (3) (Plates 5.14a & b), mounting (4) (Plates 5.1b & 5.15a) extrusion of the genitalia (5) (Plates 5.1c, 5.3b & c, 5.15b & c), and intromission (6) (Plates 5.5-5.11, Table 5.1).

Compared with conspecific trials in P. sordidus, in P. cephalotes the entire sequence leading to intromission began very soon after initial contact was made between the pair; on only a few occasions were several attempts made by the male to complete intromission.

In 70% of the trials intromission was achieved at least once, 6 pairs copulated twice and 1 pair three times within the hour. During one trial only, 20 sequences (1) (3) and (4) were completed twice but intromission was not achieved. At stage (5) the male may repeatedly extrude the genitalia and probe the female abdominal apex before the female opens the genital orifice enabling the male to insert the apex of the median lobe.

From previous observations on mating behaviour (Section 5.21) the courtship sequence may be interrupted at any stage, including stage (5) and, as already discussed, if this occurs, the sequence must be repeated from the beginning before intromission can be achieved. At all times the male is the more active in courtship, the female manifesting her receptivity by standing still. It is not known what determines female receptivity but it seems likely that she exhibits

Table 5.1 Intraspecific behaviour in P. cephalotes

<u>Behavioural Components</u>	<u>Trial Number</u>																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1. "examination" ♀ by ♂		2	4	3	2	7	5	5	2	3	7	9	5	1		3	6	2	2	5
2. "examination" ♂ by ♀	2	1											1	2	2					
3. prolonged "examination" ♀ by ♂		1	3	3	1	7	5	3		1		1	3	1		2	5	2	2	3
4. mounting		1	3	3	1	7	3	3		1			2	1		2	3	1	2	2
5. extrusion ♂ genitalia		1	3	3	1	5	2	2		1			2	1		1	2	1	2	
6. intromission		1	2	2	1	3	2	2		1			2	1		1	1	1	1	
7. ♀ aggression			1	2		1			1	3		3		1	6				4	
8. ♂ aggression			1	2		1		1	1	3		6			4				2	
9. avoidance by ♀																				
10. avoidance by ♂																				

November/December

February

Each entry represents the number of times an event was recorded.

coyness, and at each stage the male must provide the correct set of stimuli which must be accepted by the female before the sequence of courtship is continued.

Aggression between a male and female has been observed but is relatively mild, more often occurring in pairs where intromission did not occur (Table 5.1 trials 12 & 15). This is apparently caused by the female being non-receptive, whereupon she makes aggressive moves towards a courting male evoking a similar reaction from him.

In comparison with P. sordidus, the duration of intromission in P. cephalotes is short (44.625 mins (n = 8): 1.65 mins, (n = 9), Section 5.2.1), and this may be a reason why repeated copulations occurred within one trial. It is not known whether there is a critical time period between copulations, and whether this is different in the two species.

2. ♂ P. sordidus x ♀ P. sordidus (Table 5.2)

Here, as in conspecific trials with P. cephalotes preliminary behaviour (Section 5.31) was followed by examination of the female abdominal apex by the male (Plate 5.14a), (in 85% of the trials). 65% of males proceeded to stages (3) and (4). Extrusion of the male genitalia occurred in 45% of males, but in only 25% was this followed by intromission. In these trials intromission did not occur more than once, whereas in P. cephalotes intromission occurred twice or three times within a trial. This may be associated with the duration of intromission in the two species.

In comparison with females of P. cephalotes, those of P. sordidus did not remain still and often moved the apex of the abdomen sharply up and down, particularly during stage (4) where the male genitalia are extruded and the female abdominal apex is probed with the apex of the median lobe. This type of female behaviour appears to be an indicator of non-receptivity. In trials 5, 11 and 16 the male

Table 5.2 Intraspecific behaviour in P. sordidus

Behavioural Components	Trial Number																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1. "examination" ♀ by ♂		4	1	1	2	3	2	5	1	3	8	2		6	1	9		3	1	3
2. "examination" ♂ by ♀		2	1		1					1			1							
3. prolonged "examination" ♀ by ♂		1	1		2	2		1			8	1		6	1	9		3	1	3
4. mounting		1	1		2	2		1			9	1		6	1	6		4	1	1
5. extrusion ♂ genitalia					1	2					7	1		10	1	5		5	1	
6. intromission						1								1	1			1	1	
7. ♀ aggression			1	1	3	2		2	2	2	1	3	9		1	1	3		2	
8. ♂ aggression			2	1	3	2		2	2	2	1	3	18		1		3	1	1	
9. avoidance by ♀																				
10. avoidance by ♂																				

November/December

February

Each entry represents the number of times an event was recorded.

repeated stages (1),(3), (4) and (5) several times but intromission did not occur. Similarly in trials 6, 14 and 18, where intromission did occur, the sequence of behaviour prior to this was repeated several times.

As in P. cephalotes, aggression was relatively mild, more often occurring in pairs where intromission did not occur. Aggression was noted in 70% of the trials (compared with 45% in P. cephalotes) and this may be correlated with the reduced number of trials in which intromission occurred. In only one trial, 13, aggression played a major role; this type of behaviour is thought to be unusual.

Inter-specific Behaviour

3. ♂ P. cephalotes x ♀ P. sordidus (Table 5.3)

If initial contact was made between the pair (i.e. the antennae of one touched the other at any point on the body), or if the male approached the female from the rear, very brief antennation (with little movement of each individual antenna) and palpation of the female abdominal apex occurred, this was followed by marked aggression in both male and female. Thereafter, each time the pair came close together or made contact, an aggressive display followed consisting either of a series of reciprocal "attacks" or a single display by one of the pair.

A P. cephalotes male appeared to detect (visually) a P. sordidus female from 3-4 cm, once initial contact had been made. This was exhibited by the male running towards the female with mandibles open prior to an aggressive display.

In trial 7 the male grasped the female with his mandibles, around her pronotum and then around the abdomen, and did not release the struggling female. The pair were separated before the end of the trial for fear the female may be killed and the male replaced by another.

In all trials aggressive behaviour was common in 20% of the trials the female was more aggressive and the male more aggressive in 55% of the trials.

Table 5.3 Interspecific behaviour between ♂ P. cephalotes x ♀ P. sordidus

<u>Behavioural Components</u>	<u>Trial Number</u>																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1. "examination" ♀ by ♂	1	1	1	2	1		1		2	3	7	1	10	8					2	
2. "examination" ♂ by ♀											1					1			2	2
3. prolonged "examination" ♀ by ♂													4	7						
4. mounting													2	4						
5. extrusion ♂ genitalia													1	1						
6. intromission																				
7. ♀ aggression	6	3	6	2	3	3	3	4	7	1	2	3	12	3	4	1	4	4	19	5
8. ♂ aggression	8	7	6	4	3	3	12*	(2) 2	9	1	3	8	9	2	4	7	6	5	16	6
9. avoidance by ♀																				
10. avoidance by ♂																				

November/December

February

Each entry represents the number of times an event was recorded.

In two trials, 13 and 14, the P. cephalotes male displayed initial aggression towards the P. sordidus female which was reciprocated by the female. Then in both cases the male, after examining the females abdominal apex (1), proceeded to stage (2) in the sequence with prolonged and persistent examination of her dorsal and ventral abdominal surfaces. During this behaviour the female continually moved away from the male, at the same time raising her abdomen. However, the male pursued the female and used the forelegs to pull the female abdomen down, following which attempts were made by the male to mount the female. In trial 13 the male mounted the female twice and on one occasion extruded the genitalia, but the female did not remain still. The female turned her head towards the male, opening the mandibles in the aggressive "pose", and the male dismounted. In trial 14 the male mounted the female four times and extruded the genitalia once, but again the sequence of copulatory behaviour did not continue because of the counter activities of the female. Although the male was repeatedly unsuccessful in completing copulation, he continued to pursue the female, antennating and palpating her abdominal apex.

This type of behaviour is considered to be unusual; it was observed on only two occasions during the current experiments and there is no evidence for its occurrence in nature. It is possible that behaviour is affected when beetles are kept in culture conditions and this should be further investigated. All four beetles concerned had been observed to mate successfully with their respective species prior to trials 13 and 14.

At the end of trials 13 and 14 the pairs were separated. After two hours the pairs were brought together again and further observations were made. Both males made a brief examination of the females abdominal apex, (1) following which aggressive behaviour occurred. After a 24 hour separation the males of the two pairs were placed

Table 5.4 Interspecific behaviour between ♂ P. sordidus x ♀ P. cephalotes

Behavioural Components	Trial Number																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1. "examination" ♀ by ♂	1		3	1		2	2	1					1	1						
2. "examination" ♂ by ♀	1	2		1						2				3		1			3	1
3. prolonged "examination" ♀ by ♂																				
4. mounting													1							
5. extrusion ♂ genitalia																				
6. intromission																				
7. ♀ aggression		6	4		14	2	5	4	10	1	4	4	15	6	8	11	2	2	6	4
8. ♂ aggression		1	2		10	2	6	4	10	5	5	1	13	10	11	8	1	2	6	3
9. avoidance by ♀																				
10. avoidance by ♂																				1
	November/December										February									

Each entry represents the number of times an event was recorded.

Table 5.5 Summary of % occurrence of behavioural components during observation trials of intra and inter-specific behaviour in P. cephalotes and P. sordidus

		cephalotes	sordidus	cephalotes ♂	sordidus ♂
		x cephalotes	x sordidus	x sordidus ♀	x cephalotes ♀
Behavioural Components	1	90	85	65	40
	2	25	25	20	40
	3	80	65	10	0
	4	75	65	10	5
	5	70	45	10	0
	6	70	25	0	0
	7	45	70	100	90
	8	45	70	100	90
	9	0	0	0	0
	10	0	0	0	25

% Number of Trials

consecutively with two different females, and in both cases aggressive behaviour was observed. This was repeated after 72 hours and similar observations were made.

4. ♂ P. sordidus x ♀ P. cephalotes (Table 5.4)

The dominant type of behaviour observed in 90% of these trials was aggression, as in the previous set of trials with ♂ P. cephalotes x ♀ P. sordidus.

In only 40% of the trials the male was observed to briefly examine the female abdominal apex, (1). The females were observed to examine the male abdominal apex, (2), more frequently than in any of the other sets of trials. Behavioural components (3)-(6) did not occur. The female displayed more aggression in 44% of the trials, and the male more aggression in 28% of the trials. It is notable that in categories (3), (♂ P. cephalotes x ♀ P. sordidus), and (4), (♂ P. sordidus x ♀ P. cephalotes), where the dominant inter-specific reaction was aggressive, P. cephalotes was the more aggressive of the two species. This may be correlated with the greater size of P. cephalotes compared with P. sordidus.

In two trials, 1 and 4, where aggressive behaviour was not recorded from either sex initial brief examination of the partners abdominal apex, (1) and (2), was made but thereafter both remained inactive and neither of the pair reacted to the others presence.

Each interaction between a pair did not always release aggressive behaviour; on some occasions the pair remained still, side by side, and partially in contact, or one burrowed underneath the other (which has been observed to be part of a natural behavioural reaction for being beneath an object), or they climbed over one another.

Amidst aggressive displays by both sexes, in trial 13, there occurred a very brief antennation of the female abdominal apex, (1), followed by a momentary mounting of the female, (4). However, the

male antennae were not beating rapidly as is most usual and prolonged examination of the female abdominal apex, (3) did not occur. This behaviour was exhibited at a moment when the female was still and the male in a position posterior to her. The reaction of the female was not aggressive, but she walked away from the male and he did not continue to pursue the female when mounting was unsuccessful.

Inter-specific behaviour between males and females is clearly different from intraspecific behaviour, the dominant type of interaction being aggressive, except in rare cases where the male was observed to mount the female. However, it is assumed that copulation is not achieved in nature and there is no evidence that natural hybrids are formed (Section 5.6).

5.3.2 Further Observations of Interspecific Behaviour in *Philonthus* species.

1. ♂ *P. parcus* x ♀ *P. sordidus*

Background

The male *P. parcus* had been observed to mate recently with females of *P. parcus*, while the female *P. sordidus* had been kept singly for one week prior to this observation.

After placing the pair together they came into contact with each other in the face to face position, whereupon antennal fencing commenced and the male opened his mandibles to bite the mandibles, antennae and forelegs of the female in a typical aggressive display (Section 5.3). Following the first aggressive encounter the male continued to open his mandibles making a biting action while chasing the female who continually moved away from the male.

The size difference between *P. parcus* males and *P. sordidus* females is substantial, *P. parcus* being larger. This may be one of the factors by which species discrimination is carried out.

2. ♂ P. sordidus x ♀ P. parcusBackground

The female P. parcus had been observed to mate recently with males of P. parcus, while the male P. sordidus had been kept singly for one week prior to this observation.

After placing the pair together the male antennated and palpated the abdominal apex of the female. The female moved away from the male, but the male pursued her, often biting the apex of her abdomen. The female, upon detecting the male, moved rapidly away in the opposite direction without making physical contact in a typical avoidance reaction (Section 5.3).

The size difference between the two species, while less marked than in the previously mentioned case, was still obvious.

3. ♂ and ♀ P. parcus x ♂ and ♀ P. sordidusBackground

The male and female P. sordidus, which had been separated for several days, were placed together with a male and female P. parcus which had been observed to mate recently but had been separated for 15 minutes.

The males were aggressive towards one another, with their mandibles open making biting movements. Similarly, the females were aggressive towards one another. The male P. parcus exhibited very aggressive behaviour towards the female P. sordidus and also to a lesser extent towards the female P. parcus.

On a separate occasion a male and female P. parcus were placed together with a male and female P. sordidus. The male P. sordidus mounted the female P. sordidus and extruded the genitalia but was interrupted before completing copulation by an aggressive "attack" on the abdominal apex of the male P. sordidus by the male P. parcus.

5.4 Effect of Antennectomy in male Philonthus sordidus

The effect of antennectomy on mating behaviour in male P. sordidus was investigated to determine a) whether the antennae are important in detection of females prior to courtship behaviour, thereby indicating the possibility of the production of a female pheromone or contact chemical attractant, and b) their importance in stimulatory behaviour during courtship.

Owing to lack of time and shortage of stock, a number of systematically repeated experiments were not undertaken. This leaves room for much further investigation which may prove fruitful. The observations made are described in the sequence in which they occurred. Copulation never occurred in antennectomised males.

The antennae of Philonthus spp. consist of a scape, pedicel and one other basal segment which all bear long setae, and a flagellum of ten segments which also bear long setae as well as a dense covering of short fine setae. The flagellum is considered to be the main sensory part of the antenna.

1. The antennae of a male P. sordidus were cut off as near to the base as possible without damage to the head; the male was then returned to the culture box for 15 minutes. The male was then placed in an observation box in which there was a female P. sordidus and the pair were watched for one hour. There were very few encounters between the two. When the female made physical contact with the male, he rapidly raised and lowered his abdomen several times. The male did not carry out any courtship behaviour. The pair were separated after one hour.
2. After the pair had been separated for one hour, they were again placed together. Similar behaviour was observed to that in 1. The pair were separated after one hour.

3. After a further hour of separation the same male was placed together with a different female. When the female abdominal apex made contact with the male mouthparts and antennal stumps, the male briefly palpated and beat the antennal stumps on the terminal abdominal tergites. This was repeated a second time. The male only performed this behaviour when the female had first made physical contact with him, suggesting that vision is not employed in the detection of the female. During the examination (Section 5.21) of the female abdominal apex by the male, he did not assume the usual posture of a courting male at this time (Plates 5.1b & 5.15a). Before moving away from the female the male raised the pro-thoracic legs onto the sides of the abdomen in a way which resembled the start of leg-rubbing behaviour at the beginning of mounting.

The most common type of behaviour which otherwise occurred involved the male moving rapidly away from the female each time she made contact with him.

4. After a further separation the same male was placed with a third female. If the female abdominal apex came into contact with the male mouthparts, palpation and "antennation" was carried out. This occurred several times indicating a particular attractiveness of the female, nevertheless on each occasion after a few seconds the female moved away from the male. After one hour, the antennectomised male was replaced by a normal male to ascertain whether this female was receptive. Immediately the normal male antennated and palpated the female abdominal apex and mounted her. However, before intromission took place the normal male was once again replaced with a different antennectomised male. When this male encountered the female, face to face, an aggressive display occurred (Section 5.3). However, when contact was made with the female abdominal apex the male immediately palpated and "antennated" the terminal tergites which was followed by

rubbing the pro and meso-thoracic legs against the sides of the abdomen in the preliminary part of mounting. At this stage the female walked away from the male. This occurred a second time a few seconds later but was interrupted at the same stage. It is thought that vigorous antennation over the female dorsum is a necessary stimulation during all the preliminary stages of courtship behaviour. This type of stimulation is not possible in an antennectomised male and this may be a reason why courtship was interrupted in an obviously receptive female.

It is suggested that an antennectomised male uses the maxillary palps more (to compensate for the loss of the antennae) since, during examination of the female abdominal apex, the mandibles were opened wide and the maxillary palps extended well forwards and vibrated in the air over the terminus of the female. Mounting often followed this type of behaviour.

5. After separation the second antennectomised male was placed together with a new female. The same movement of the maxillary palps was observed each time the female abdominal apex was close to male mouthparts.

6. (The same pair as in 5. after a short separation). Mounting by the male was observed but was interrupted at the same stage as in 4.

7. After a weeks isolation the second antennectomised male was placed together with a different female. No courtship or aggressive behaviour was observed over a period of 30 minutes. A normal male was then placed in the box with the pair. On coming into contact with the female the normal male antennated and palpated her abdominal apex. On arriving face to face with the antennectomised male, the second male moved to his abdominal apex, antennated, palpated and mounted the male and extruded the genitalia whilst attempting to achieve intromission. Throughout this homosexual mating attempt, the antennectomised male remained still, apart from moving his legs up and down. The male made 10 attempts to insert the genitalia into the other

male. Eventually the normal male moved away from the male and made an aggressive display towards the female which was immediately followed by courtship and intromission.

Further antennectomised males were placed together with different females and, apart from aggression, no further behaviour of significance was observed.

To conclude, it is suggested that a receptive female produces a chemical attractant which is perceived by the male only at close quarters and is not a long range pheromone. The chemical is detected by the male antennae at a distance of less than a centimetre and by the maxillary palps on contact. Vision plays only a very minor role in detection of females if at all.

5.4.1 Reaction of antennectomised and normal male *Philonthus sordidus* to freshly crushed females.

To ascertain further whether the female produces a chemical attractant, the behaviour of an antennectomised and normal male towards a freshly crushed female was observed. If abdominal scent glands are present in the female, a chemical not being produced at the time the female is alive should be released upon crushing the glands. However, if the attractant is only produced after a chemical reaction from precursors within the gland, crushing may not necessarily release the correct compound.

The female was crushed onto filter paper in the centre of an observation box. The two males were added to the box and their behaviour observed. There was no immediate reaction by either male, both stood still for a few seconds and then walked around the perimeter of the box. The normal male then approached the female and began to eat her, the antennectomised male then did the same. There was no hint of antennation or the type of courtship behaviour which is triggered by a receptive female.

Further investigation is obviously necessary to establish the presence of an attractant.

5.4.2 Pairs in copula

Pairs of species in copula have been examined to establish the position of the genitalia and prominent setae of the terminal abdominal segments. These are illustrated in Omalium rivulare (Figs. 5.1 & 5.2), Quedius humeralis (Figs 5.3 & 5.4), Philonthus cephalotes (Fig. 5.5) and P. parcus (Fig. 5.6).

Fig.5.1 Diagram to show the position of the genitalia in Omalium
rivulare in copula.

- a) ♀ dorsal, ♂ lateral
- b) ♀ ventral, ♂ lateral

chitinised parts of female genitalia - black
chitinised parts of male genitalia - shaded

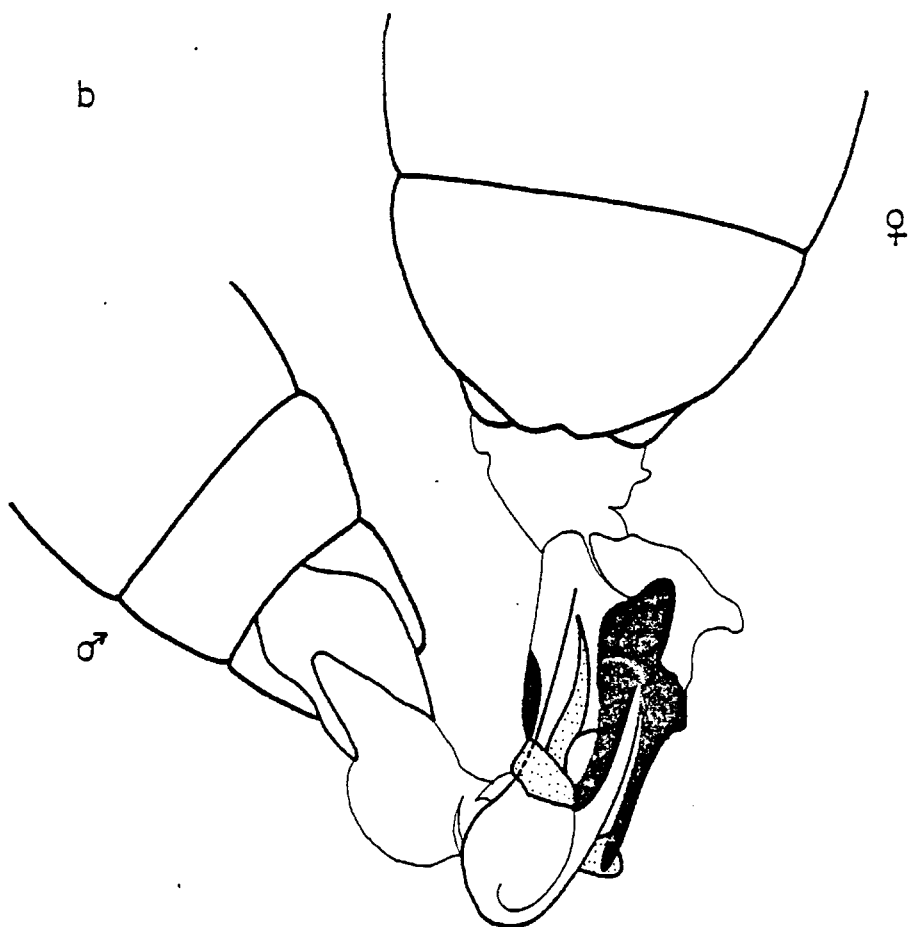
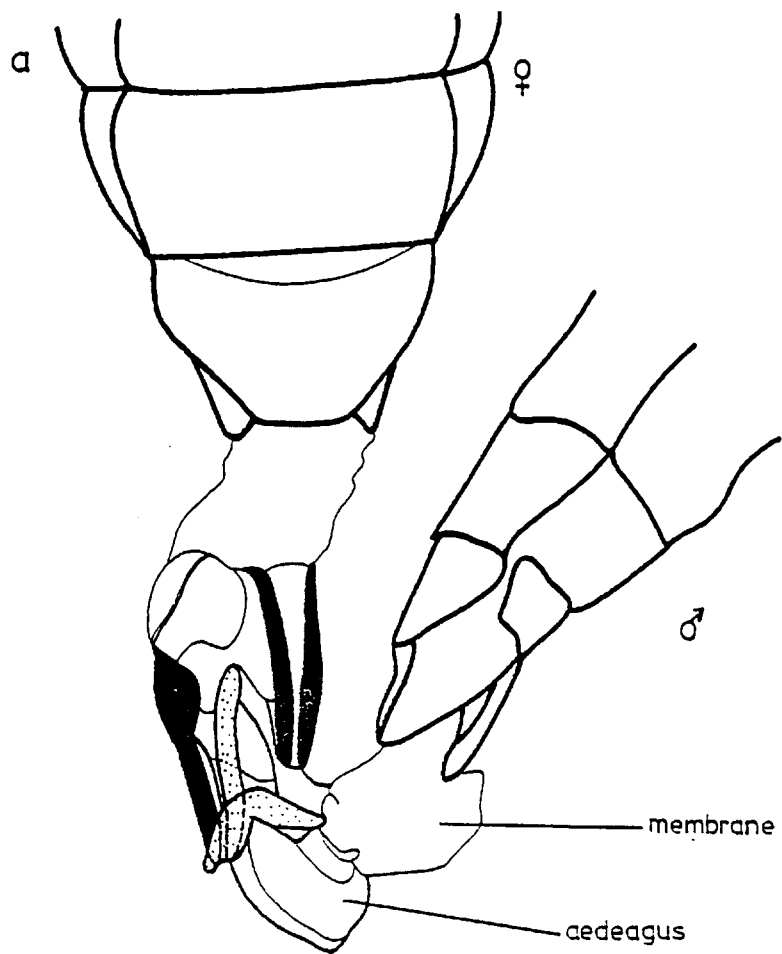


Fig.5.2 Male and female genitalia of Omalium rivulare following separation after intromission.

- a) female, dorsal view
- b) female, lateral view
- c) male, dorsal view
- d) male, lateral view

chitinised parts of genitalia - shaded

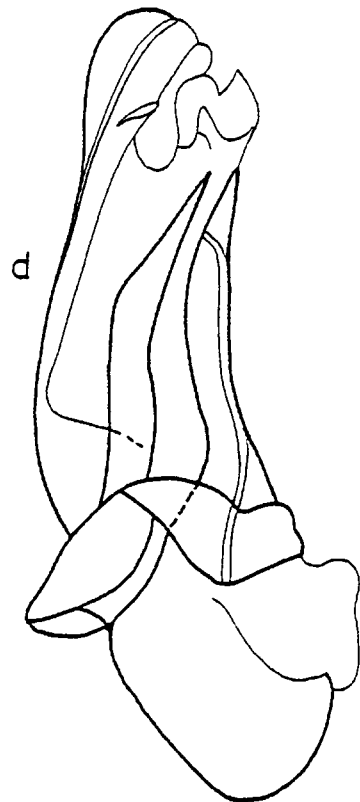
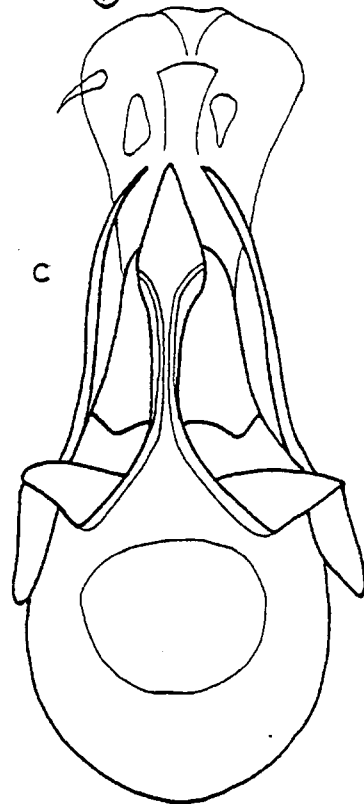
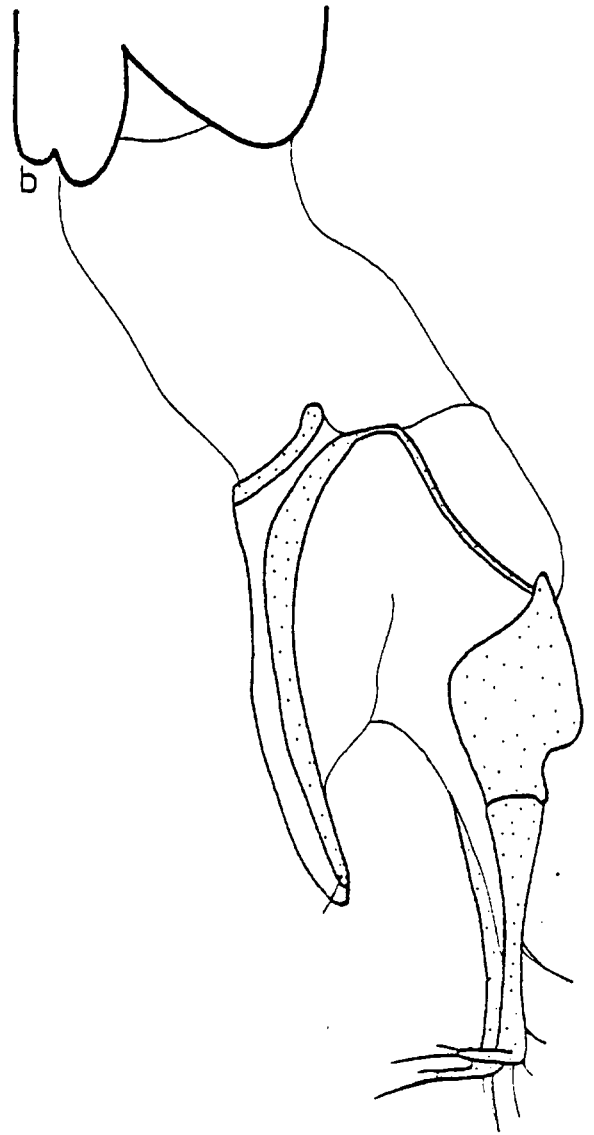
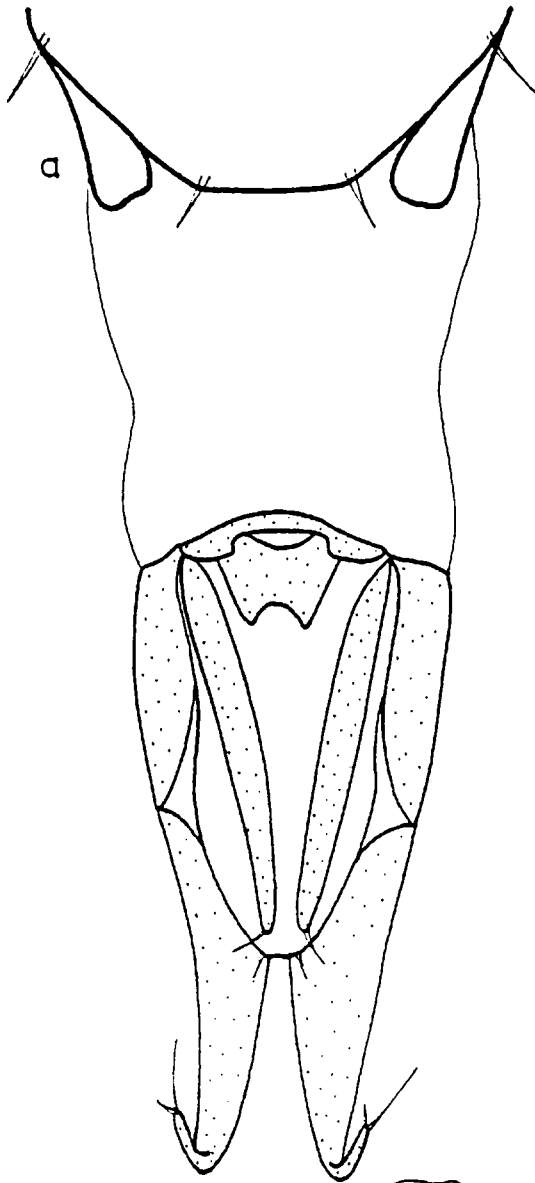


Fig.5.3 Diagram to show the position of the genitalia(setae excluded)
in Quedius humeralis in copula.

a) ♂ ventral, ♀ dorsal

b) ♂ ventral, ♀ dorsal with tergite and sternite VIII removed

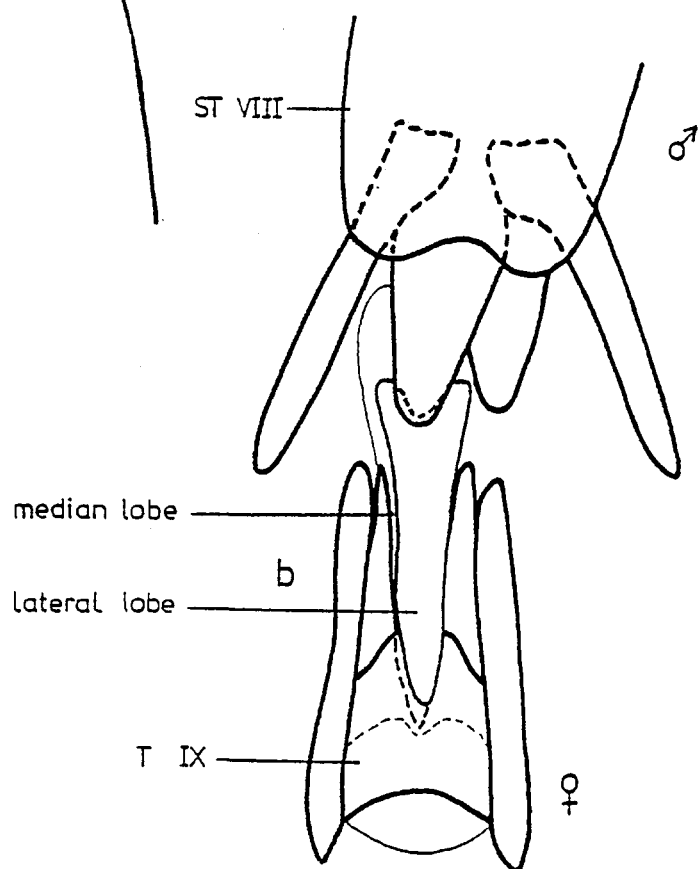
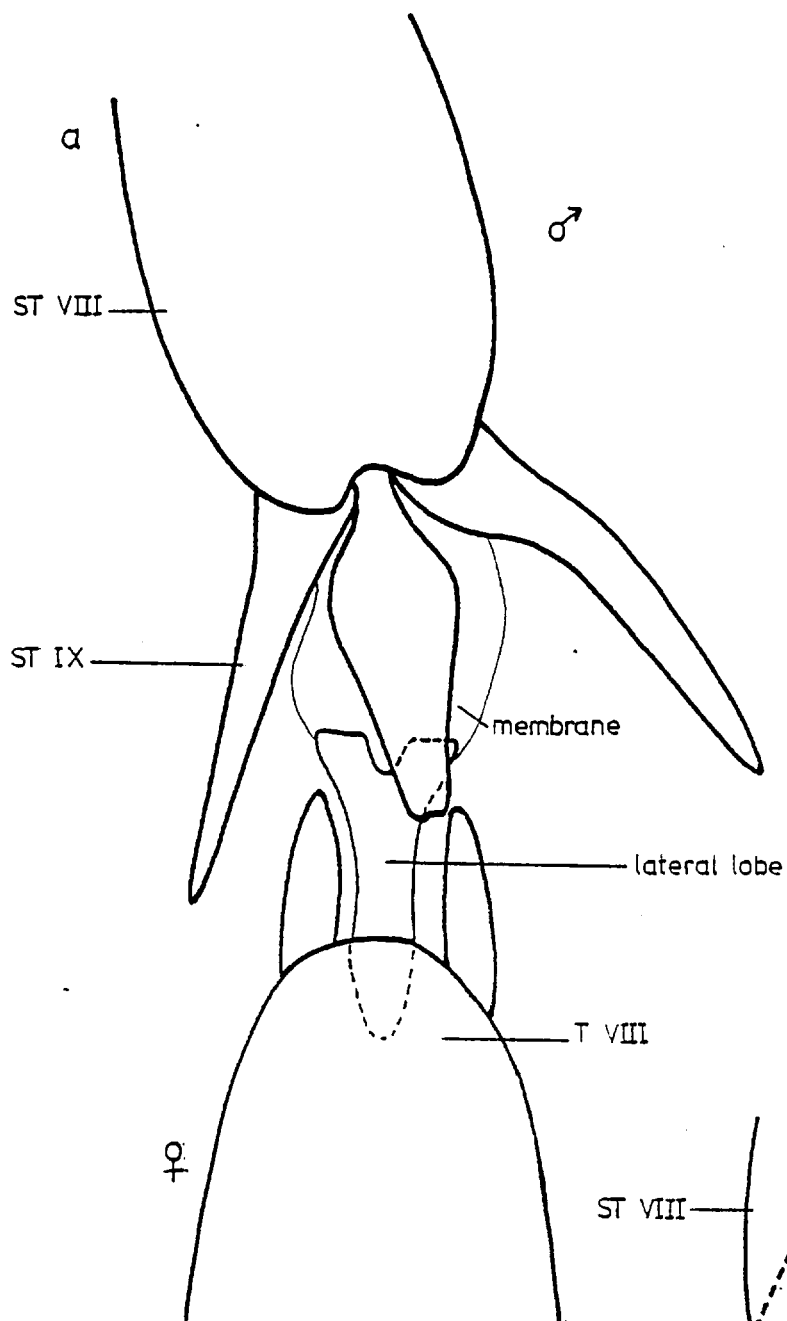


Fig.5.4 Diagram to show the position of the genitalia (setae excluded)

in Quedius humeralis in copula.

♀ ventral, ♂ dorsal

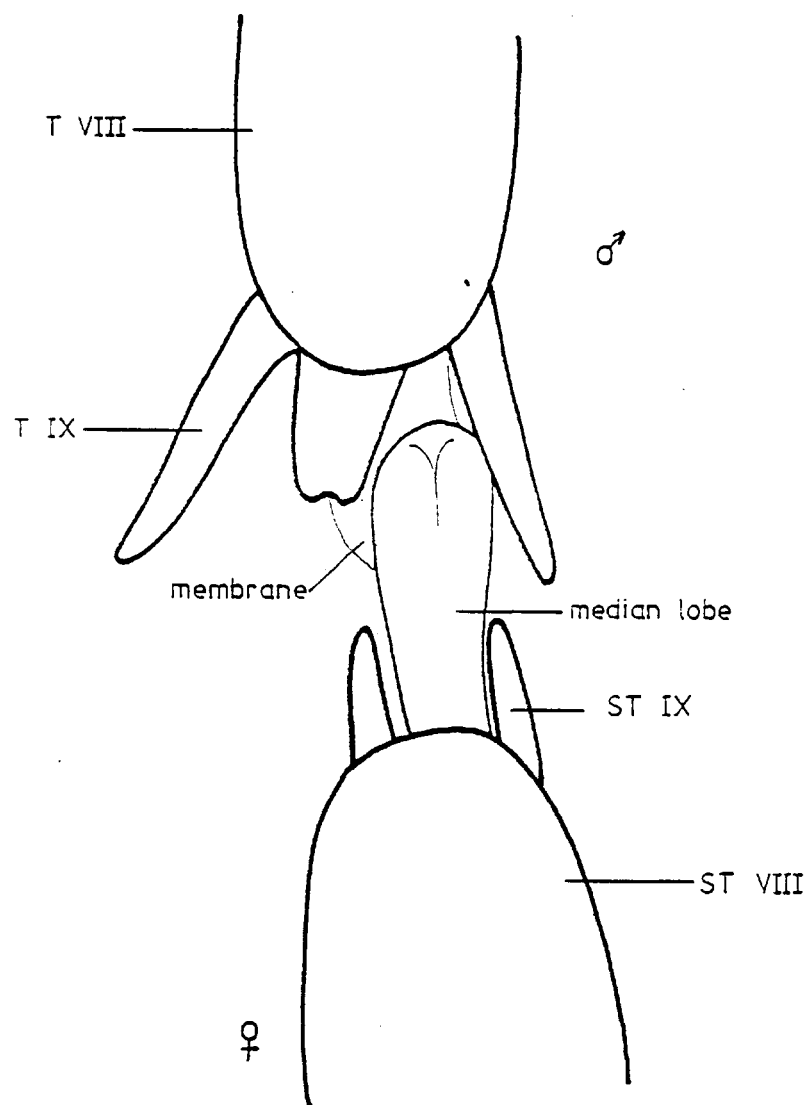


Fig.5.5 Diagram to show the position of the genitalia and prominent setae of the terminal abdominal segments of Philonthus cephalotes in copula.

- a) ♀ ventral, ♂ dorsal
- b) ♀ dorsal, ♂ ventral

setae shown on one side only

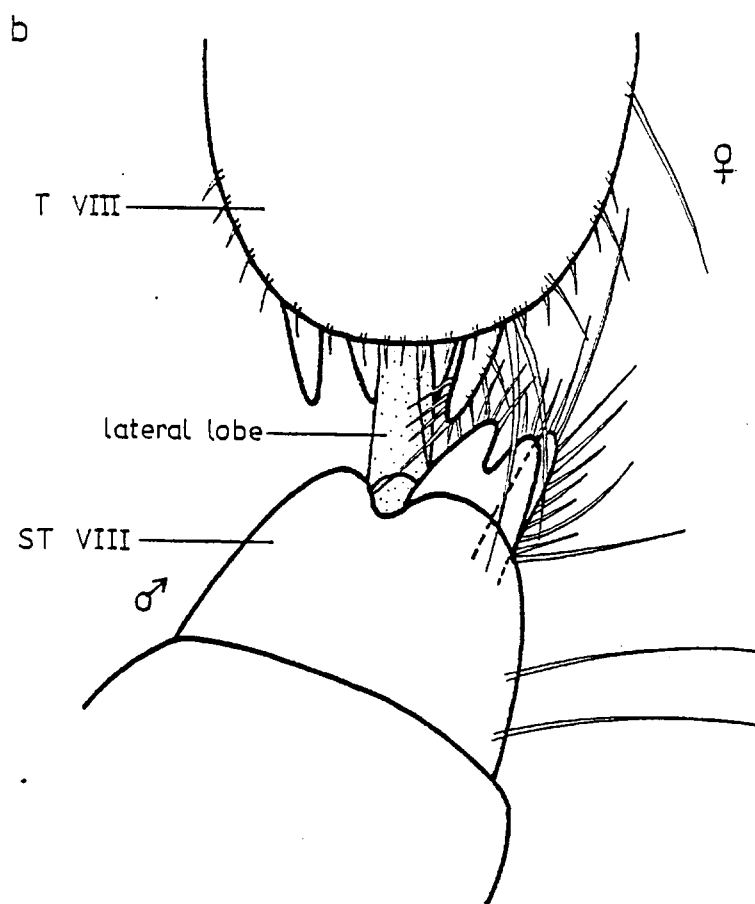
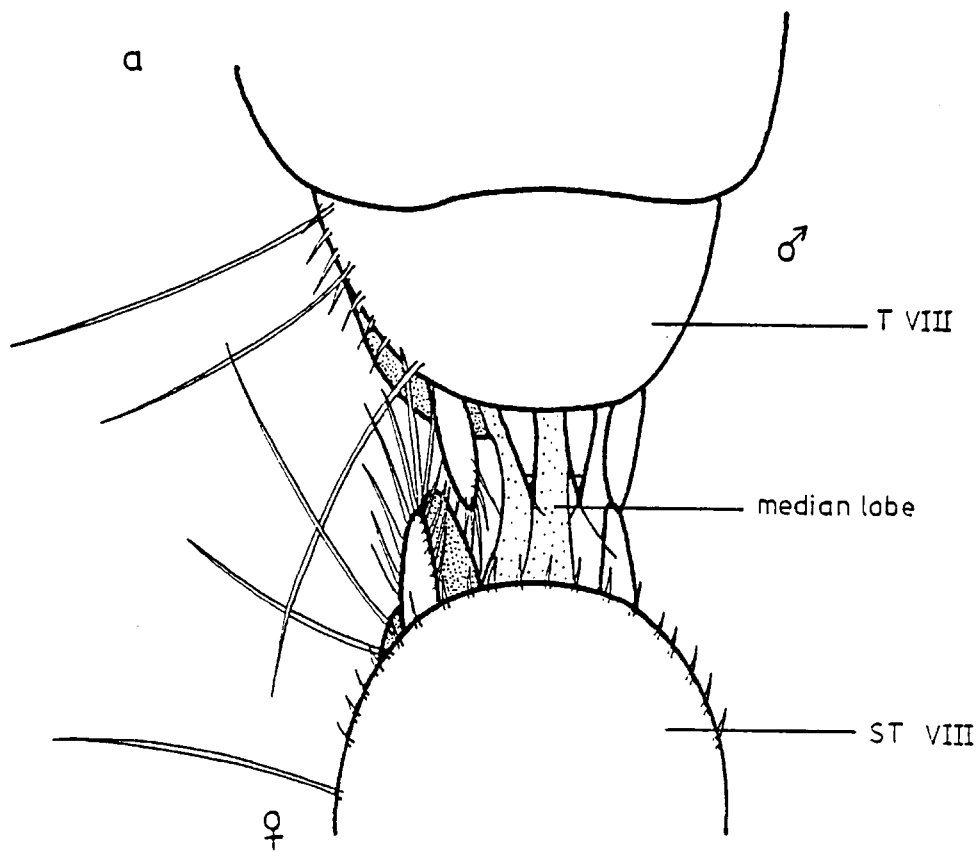
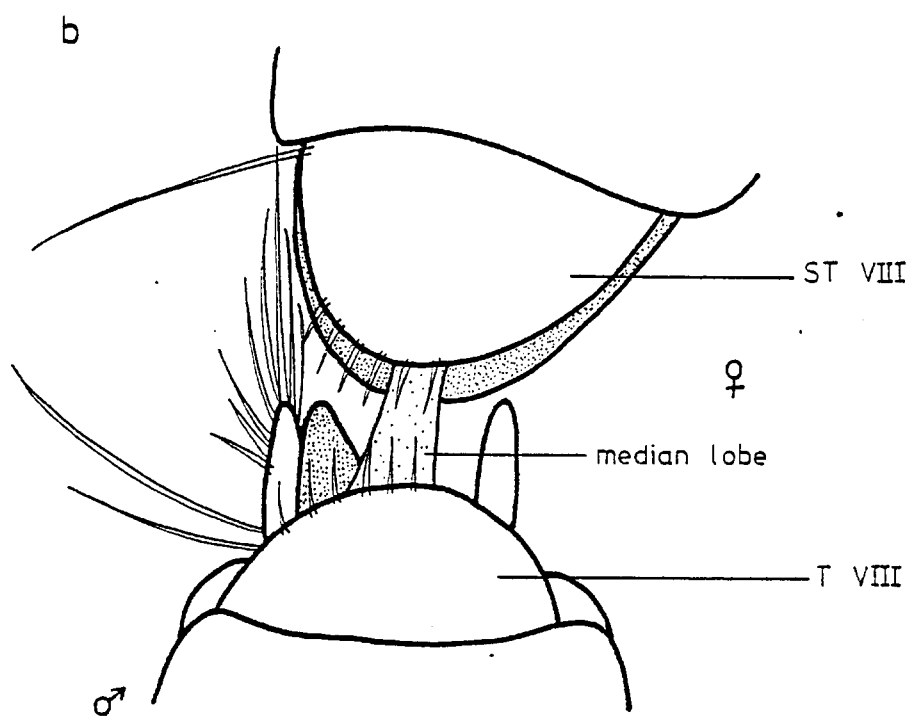
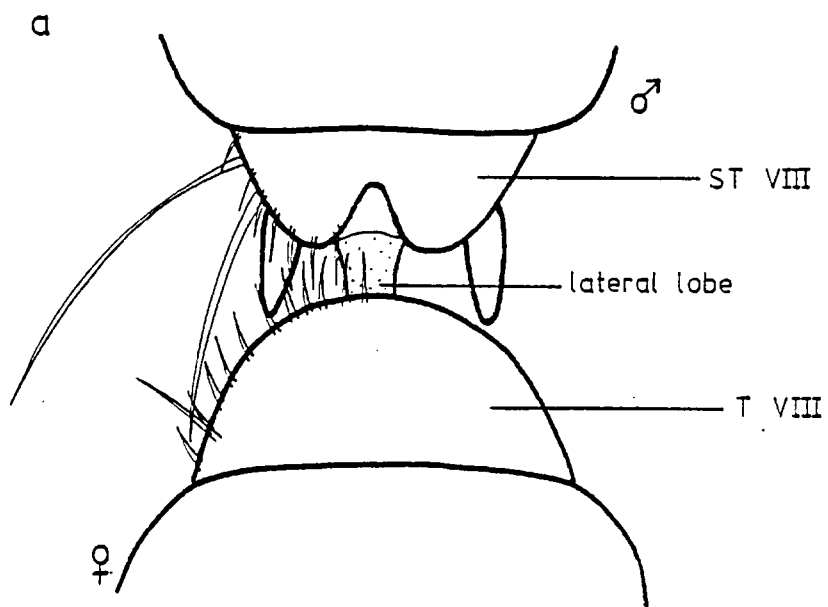


Fig.5.6 Diagram to show the position of the genitalia and prominent setae of the terminal abdominal segments of Philonthus parvus in copula.

a) ♀ dorsal, ♂ ventral

b) ♀ ventral, ♂ dorsal

setae shown on one side only



5.5 Mating Behaviour Review

The following review is taken from the literature (source Zoological Record 1899-1974, Entomology Abstracts - 1979 and other varied sources). The review is composed systematically and each family, in which there is information on mating behaviour, is treated separately. The concluding discussion (Section 5.52.42) summarises the data together with the different types of signal used to communicate between the sexes during courtship and mating.

The species in which there is information on mating behaviour in the literature are listed systematically (Section 5.52). The most recent nomenclature is adopted and this is derived from catalogues in the BMNH which are based upon the Coleopterorum Catalogus series (publ. W. Junk). Abbreviations are used in the list to indicate the type of information contained within a reference.

- C - courtship behaviour
- S - stimulatory behaviour by the male during mating
- 2^o - secondary sexual characters
- R - recognition (in the broad sense)
- I - reproductive isolation

Where the abbreviations are absent, this type of information cannot be found in the reference.

The classification of the Coleoptera follows an unpublished scheme by J.F.Lawrence.

5.5.1 SYSTEMATIC INDEX OF SPECIES FOR WHICH INFORMATION ON MATING
BEHAVIOUR IS AVAILABLE

ADEPHAGA

CARABIDAE

CICINDELINAE

<u>Cicindela</u> spp.		Zikan 1929
<u>Prepusa</u> sp.		"
<u>Euprosopus</u> sp.		"
<u>Iresia</u> sp.		"
<u>Odontochila</u>	"	"
<u>Oxychila</u> sp.		"
<u>Tetracha</u> sp.		"
<u>Omus dejeani</u> Rche.		Pratt 1939
<u>Cicindela circumpicta</u> Lafeate	2°	Willis 1967
<u>C. duodecimguttata</u> Dej.	S	Moore 1906
<u>C. flavopunctata</u> Chevr.		Mitchell 1902
<u>C. flavopunctata rectilatera</u> Chaud.		Balduf 1969
<u>C. fulgida</u> Say	2°	Willis 1967
<u>C. nevadica</u> Lec.	2°	"
<u>C. oregana</u> Lec.		Maser 1976
<u>C. punctulata</u> Ol.		Goldsmith 1916
<u>C. purpurea</u> Ol.	S	Moore 1906, Shelford 1908, Balduf 1969
<u>C. scutellaris</u> Say		Mitchell 1902, Balduf 1969
<u>C. togata</u> Laf.	2°	Willis 1967

BRACHININAE

<u>Brachinus pallidus</u> Erwin	S	Erwin 1967
<u>B. sclopeta</u> F.		Wautier and Wautier 1967

CARABINAE

<u>Calosoma sycophanta</u> L.		Balduf 1969
<u>Carabus</u> spp.		Leitner 1943, Larochelle 1972a & b
<u>C. auratus</u> L.	S	Balduf 1969
<u>C. cancellatus</u> Ill.	S	Kirchner 1927, Leitner 1943, Balduf 1969
<u>C. nemoralis</u> Müller	S2°	Delkeskamp 1930, Leitner 1943, Balduf 1969.
<u>Nebria</u> spp.		Larochelle 1972a & b
<u>N. complanata</u> L.	CS	King and Stabins 1971
<u>N. purpurata</u> Lec.		Kavanaugh and Martinko 1972
<u>Blethisa</u> spp.		Larochelle 1972a
<u>Pasimachus elongatus</u> Lec.	S2° I	Cress 1966
<u>P. punctulatus</u> Hald.	S2° I	Alexander 1959
<u>Scarites substriatus</u> Hald.	CS	Hlavac 1967
<u>Broscus cephalotes</u>		Michelsen 1963
<u>Aphaenops lambensi</u>		Cabidoche 1972
<u>Trechus cardioderus</u> Putz		Leitner 1943
<u>T. noricus</u> Meixn.	I	"
<u>T. ovatus</u> Putz	I	"
<u>T. regularis</u> Putz	I	"
<u>Bembidion</u> spp.		Larochelle 1972a & b
<u>Asaphidion flavipes</u> L.	S2°	Bauer 1971
<u>Amara</u> spp.		Larochelle 1972a & b
<u>Pterostichus</u> spp.		Larochelle 1972a & b
<u>P. chalcites</u> Say		Larochelle 1973

<u>P. cristatus</u> Duf.			Witzke 1973
<u>P. niger</u> Schaller	S2°	I	"
<u>P. nigrita</u> Payk.			"
<u>P. vulgaris</u> L.			"
<u>Harpalus</u> spp.			Larochelle 1972a & b
<u>Harpalus pubescens</u>			Witzke 1973

HALIPLIDAE

<u>Haliphus wehnkei</u> Gerh.	S2°		Beier 1929
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DYTISCIDAE

COLYMBETINAE

<u>Colymbetes fuscus</u> L.	2°		Balduf 1969
<u>Rhantus atricolor</u> Aube	C 2°	RI	Balduf 1969, Smith 1973
<u>R. binotatus</u> Harris	C 2°	RI	"
<u>R. gutticollis</u> Say	C 2°	RI	"
<u>Agabus undulatus</u> Schr.			Balduf 1969

DYTISCINAE

<u>Dytiscus</u> spp.			Leitner 1943
<u>D. dimidiatus</u> Bergstr.			Balduf 1969
<u>D. marginalis</u> L.	CS 2°	R	Scheidt 1909, Blunck 1912a,b&c, Balduf 1969
"	2°		Brocher 1926
<u>D. marginalis</u> v <u>conformis</u> Kunze	2°		Scheidt 1909

CYBISTRINAE

Balduf 1969

GYRINIDAE

ENHYDRINAE

Dineutes americanus Say

Balduf 1969

D. horni Rbts.

"

D. nigrior Rbts.

"

GYRININAE

Gyrinus natator L.

2°

Hatch 1925,
Balduf 1969.G. substriatus Steph.

Balduf 1969

ORECTOCHILINAE

Orectochilus villosus Muller

Balduf 1969

POLYPHAGA

SILPHIDAE

SILPHINAE

Necrodes surinamensis F.

S R

Ratcliffe 1972

Silpha atrata L.

Balduf 1969

Dendroxena quadrimaculata Scop.

Balduf 1969

NICROPHORINAE

Nicrophorus spp.

CS

"

STAPHYLINIDAE

Voris 1934

OMALIINAE

Eusphalerum spp.

C

Blum 1976

TACHYPORINAE

Tachinus signatus Grav.Lipkow 1966,
see Section 5.2.14Tachyporus spp.

"

ALEOCHARINAE

see Section 5.2.16

MYRMEDONIINI

Lomechusoides strumosa F.Donisthorpe 1908,
1927, Balduf 1969Lomechusa emarginata Payk.Donisthorpe 1927,
Balduf 1969L. paradoxa Grav.Keys 1914,
Donisthorpe 1927,Zyras spp.Donisthorpe 1927
Balduf 1969Velleius dilatatus F.

Balduf 1969

DINARDINI

Dinarda spp.

Donisthorpe 1927

ALEOCHARINI

Aleochara spp.

Welch 1964

A. bilineata Gyll.Colhoun 1953,
Fuldner 1960,
Balduf 1969A. bipustulata L.

Fuldner 1960

A. curtula Goeze

S2° RI

Kemmer 1926,
Balduf 1969,
Blum 1976,
Peschke 1978aCypha longicornis Payk.

see Section 5.2.15

OSORIINAE

Osorius planifrons Lec.

Smith et al 1978

STENINAE

Stenus spp.

Michelsen 1963

STAPHYLININAE

STAPHYLININI

STAPHYLININA

Creophilus maxillosus L.

S

Fichter 1949,
Kramer 1955Staphylinus olens Müller

Nield 1976

QUEDIINA

<u>Quedius</u> <u>curtipennis</u> Grav.	Frank 1968
<u>Q.</u> <u>fuliginosus</u> Grav.	"
<u>Q.</u> <u>fumatus</u> Steph.	"
<u>Q.</u> <u>lateralis</u> Grav.	"
<u>Q.</u> <u>longicornis</u> Kraatz	"
<u>Q.</u> <u>picipes</u> Mann.	"
<u>Q.</u> <u>mesomelinus</u> Marsh.	see Section 5.2.8
<u>Q.</u> <u>tristis</u> Grav.	see Section 5.2.9

PHILONTHINA

<u>Philonthus</u> <u>cephalotes</u> Grav.	see Section 5.2.1
<u>P.</u> <u>dicoideus</u> Grav.	see Section 5.2.2
<u>P.</u> <u>fimetarius</u> Grav.	see Section 5.2.3
<u>P.</u> <u>longicornis</u> Steph.	see Section 5.2.4
<u>P.</u> <u>marginatus</u> Strom.	see Section 5.2.5
<u>P.</u> <u>parcus</u> Sharp	see Section 5.2.1
<u>P.</u> <u>politus</u> L.	see Section 5.2.6
<u>P.</u> <u>sordidus</u> Grav.	see Section 5.2.1
<u>P.</u> <u>tenuicornis</u> Muls. & Rey	see Section 5.2.7

OXYTELINAE

<u>Oxytelus</u> <u>sculptus</u> Grav.	see Section 5.2.13
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SCYTMAENIDAE

Brown & Crowson 1980

HYDROPHILIDAE

SPERCHEINAE

<u>Spercheus</u> <u>emarginatus</u> Schaller	S	Baldur 1969
--	---	-------------

HYDROCHINAE

HELOPHORINAE

<u>Helophorus</u> spp.	I	Angus 1970
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BEROSINAE

Berosus spp.

Van Tassel 1965

Berosus punctatissimus salvini
Sharp

CS

"

HYDROBIINAE

Hydrobius fuscipes L.

CS

Balduf 1969

Hydrous triangularis Say

2°

"

HISTERIDAE

Hister bipustulatus Schrank.

C

Lierath 1955

HELODIDAE

Cyphon coarctatus Payk.

CS 2°

Nyholm 1969, 1972a & b

LUCANIDAE

Platycerus virescens F.

S

Mathieu 1969

Dorcus parallelus Say

S 2°

"

Lucanus capreolus L.

S 2° R

"

L. cervus L.

2° R

Brull 1952

L. placidus Say

S 2° R

Mathieu 1969

Ceruchus piceus Web.

S

"

PASSALIDAE

Odontotaenius disjunctus Illiger

S

Schuster 1975

O. striatopunctatus Perch

S

"

O. zodiacus Truq.

S

"

Passalus affinis Perch

S

"

P. convexus Dalm.

S

"

P. punctiger St. Farg et Serv.

S

"

SCARABAEIDAE

SCARABAEINAE

SCARABAEINI

<u>Scarabaeus sacer</u> L.	R	Halffter & Matthews 1966
<u>S. semipunctatus</u> F.	R	"
<u>Canthon pilularis</u> L.	R	"
<u>Sisyphus schaefferi</u> L.	R	"

COPRINI

<u>Copris hispanus</u> L.	R	"
<u>Phanaeus daphnis</u> Har.	SR	Halffter & Matthews 1966, Halffter & Lopez 1977
<u>P. nimrod</u> Har.	SR	Halffter & Matthews 1966
<u>Pinotus carolinus</u> L.	R	"
<u>Gymnopleurus geoffroyi</u> Fuessl.	R	"
<u>G. mopsus</u> Pall.	R	"

ONTHOPHAGINI

<u>Onthophagus</u> spp.	R	"
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APHODIINAE

<u>Aphodius distinctus</u> Muller	"	Schmidt 1935
<u>A. fimetarius</u> L.	"	"
<u>A. prodromus</u> Brahm	"	"

RUTELINAE

RUTELINI

<u>Cotalpa granicollis</u> Hald.		Jorgensen 1963
<u>C. puncticollis</u> Lec.	R	Cheary et al 1972
<u>Anisoplia tempestiva</u> Er.	R	Pilleri 1966

ANOMALINI

<u>Popillia japonica</u> Newm.	SR	Ladd 1970, Barrows & Gordh 1978
<u>Phyllopertha horticola</u> L.	R	Rittershaus 1927, Milne 1960

<u>Anomala aenea</u> Deg.		Rittershaus 1927
MELOLONTHINAE		
<u>Melolontha melolontha</u> <u>vulgaris</u> F.		Weber 1915
<u>M. melolontha</u> L.	S	Landa 1960
<u>Macroductylis</u> spp.	S R	Bennett 1974, Ritcher 1958
<u>Hoplia</u> spp.		Ritcher 1958
<u>Rhizotrogus aequinoctialis</u> Herbst	R	Ivashchenko et al 1972
<u>Amphimallon assimilis</u> Herbst	R	Rittershaus 1927
<u>A. majalis</u> Razoum	S R	Menees 1963
<u>Holotrichia insularis</u> Reiche		Srivastava & Khan 1963
DYNASTINAE		
<u>Strategus aloeus</u> L.		Beebe 1944
<u>Ligyris</u> sp.		Ritcher 1958
<u>Metanastes</u> sp.		"
<u>Heteronychus</u> sp.		"
<u>Megasoma elephas</u> F.		Beebe 1944
<u>Pericoptus truncatus</u> F.		Dale 1963
TRICHIINAE		
<u>Trichotinus assimilis</u>		Hoffman 1935, Ritcher 1958
<u>T. piger</u>	S	"
<u>Trigonopetastes</u> sp.		"
VALGINAE		
<u>Valgus</u> sp.		"
CETONIINAE		
GEOTRUPINAE		
<u>Geotrupes mutator</u> Marsh	C R	Teichert 1955
<u>G. stercorarius</u> L.		"

<u>Pleocoma hirticollis</u> <u>vandykei</u> Linsley	R	Page & Fischer 1976
BUPRESTIDAE		
ACMAEODERINAE		
<u>Polycester abdita</u> Barr	R	Beer 1970
BUPRESTINAE		
<u>Hippomelas planicosta</u> Lec.	S R	Alcock 1976
<u>Hesperorhipis</u> sp.	R	Wellso 1966
<u>Trichinorhipis</u> sp.	R	"
<u>Xenorhipis brendeli</u> Lec.	R	"
<u>Buprestis rutstica</u> L.	R	Lejfelt & Lejfelt 1978
<u>Chrysobothris</u> sp.	R	Beer 1970
AGRILINAE		
<u>Agrilus acutus</u> F.	S R I	Dutt 1969
<u>A. anxius</u> Gory	S R I	Carlson & Knight 1969
<u>A.g:liragus</u>	S R I	"
<u>A. horni</u> Kerr	S R I	"
<u>Pseudocotalpa giulianii</u> Hardy	S R	Hardy 1976
ELATERIDAE		
AGRYPNINAE		
<u>Pyrophorus atlanticus</u> Hyslop	R	Lloyd 1965
<u>P. pelluscens</u> Eschtz.		"
ANTOINAE		
<u>Ctenicera aeripennis</u> <u>destructor</u> Brown	R	Zacharuk 1958
EUCNEMIDAE		
<u>Melasis buprestoides</u> L.		Palmqvist 1952
LYCIDAE		
LYCINAE		
CALOPTERINI		

<u>Calopteron terminale</u> Gerh.		Burke 1976
METRIORRHYNCHINI		
<u>Metriorrhynchus semiflabellatus</u>		Poulton 1913
DRILIDAE		
<u>Drilus flavescens</u> Oliv.		Balduf 1969
<u>D. mauritanicus</u> Luc.		"
PHENGODIDAE		
LAMPYRIDAE		
LUCIOLINAE		
<u>Luciola</u> spp.		Lloyd 1973 a
<u>Pteroptyx</u> spp.	R I	Lloyd 1973 a
LAMPYRINAE		
<u>Lampyris knulli</u> Green		Lloyd 1966
<u>L. noctiluca</u> L.		Balduf 1969, Lloyd 1972
<u>Lamprophorus tenebriosus</u> Walk.		Balduf 1969
<u>Pyraclomena dispersa</u> Green	S	Lloyd 1964, 1966
<u>Lecontea angulata</u> Say		Lloyd 1966
<u>L. borealis</u> Rand.		"
<u>L. lucifera</u> Melsh.		"
<u>L. marginalis</u> Green		"
<u>Photinus</u> spp.		Balduf 1969
<u>P. marginellus</u> Lec.		"
<u>P. marginellus</u> v. <u>castus</u> Lec.		"
<u>P. pyralis</u> L.		"
<u>P. scintillans</u> Say		"
<u>P. greeni</u>		Buck & Buck 1972
<u>P. concissus</u> Lloyd		Lloyd 1968
<u>Phausius reticulata</u> Say		Lloyd 1965
<u>Luciola obsoleta</u> Oliv.		Lloyd 1972
<u>Lucidota fenestralis</u>		Balduf 1969

PHOTURINAE

Photuris pensylvannica Geer

Baldur 1969

CANTHARIDAE

CANTHARIDAE

MALTHINAE

Malthinus flaveolus Herbst

see Section 5.5.2.20

CANTHARINAE

Cantharis cryptica Ashe

"

C. fulvicollis F.

"

C. nigricans Mull.

"

Rhagonycha flaveolus Herbst

"

R. fulva Scop.

"

R. limbata Thoms.

"

DERODONTIDAE

Laricobius erichsoni Rosenh.

Clark & Brown 1958

DERMESTIDAE

ANTHRENINAE

Trogoderma glabrum Herbst

S R

Wojcik 1969a & b,
Vick 1973, Hammack &
Burkholder 1976T. granarium Everts

S R

Hadaway 1956, Finger
et al 1965, Karnarvar
1972, Chaudhari & Kapil
1976, Levinson et al
1970T. grassmani Beal

S R

Beal 1954

T. inclusum Lec.

S R

Hadaway 1956, Vick et al
1972, Vick 1973T. maderae

S R

Beal 1954

T. simplex Jayne

S R

"

T. sternale Jayne

S R

"

T. tarsale Melsh.

S R

Woodsdalek 1912

T. variabilis Ballion

S R

Beal 1954

Anthrenus flavipes Lec.

S R

Wojcik 1969 a & b

BOSTRICHIDAE

DINODERINAE

Dinoderus ocellaris

Aziz & Sitarman 1948

LYCTINAE

Lyctus plannicollis Lec.

Wright 1960

PSOINAE

Psoa maculata Lec.

Tilden 1953

ANOBIIDAE

Ptilinus ruficornis Say

R

Acciavatti 1972

ERNOBIINAE

Ernobius consimilis

Sharp 1916

E. mollis L.2^o

Sharp 1916

XYLETINAE

Lasioderma serricorne F.

R

Tobin & Smith 1971,
Coffelt 1971

PTINIDAE

Ptinus clavipes Panzer

C

Woodroffe 1958

CLERIDAE

CLERINAE

Baldus 1969

Enoclerus lecontei Wolc.

Berryman 1966

CORYNETINAE

Necrobia rufipes Deg.

R

Hitchcock 1963

MELYRIDAE

MALACHIINAE

Malchius aeneus L.S2^o R

Matthes 1962b

M. bipustulatus L.S2^o R

" 1962a & b

M. elegansS2^o R

" 1962b

M. marginellus Ol.S2^o R

" 1962b

M. viridis F.S2^o R

" 1962a

Collops vittatus SayS2^o RMcAtee 1916,
Nielson & Henderson 1959

<u>Anthocomus fasciatus</u> L.	S2° R	Matthes 1962b
<u>A. rufus</u> Berbst	S2° R	Matthes 1962b, 1971
<u>Axinotarsus marginalis</u> Lap.	S2° R	Matthes 1962b
<u>A. pulicarius</u> F.	S2° R	" 1962a & b
<u>Troglops albicans</u>	S2° R	" 1962a & b
CUCUJIDAE		
LAEMOPHLOETINAE		
<u>Cryptolestes ferrugineus</u>	S R	Wojcik 1969a & b
<u>C. pusillus</u>	S R	"
SILVANINAE		
<u>Oryzaephilus mercator</u> Fauv.	S R	"
CRYPTOPHAGIDAE		
CRYPTOPHAGINAE		
<u>Cryptophagus acutangulus</u> Gyll.	S	Hinton & Stephens 1941
ATOMARIINAE		
<u>Atomaria ruficornis</u> Marsh.		Evans 1961
COCCINELLIDAE		
SCYMNINAE		
<u>Stethorus pauperculus</u> Weise		Puttaswamy & Channa Basavanna 1977
COCCINELLINAE		
<u>Cycloneda sanguinea</u> L.		Hodek 1967
<u>Rodolia cardinalis</u> Muls.		"
<u>Coleophora swinhoei</u> Cr.		Balduf 1969
<u>Callineda teshidinaria</u> Muls.		"
<u>Olla abdominalis</u> Say		"
<u>Hippodamia convergens</u> ab. <u>ambigua</u> Lec.	I	"

<u>Coccinella septempunctata</u> L.		Balduf 1969,
<u>C. transversoguttata</u> ab.		Wang <u>et al</u> 1977
<u>californica</u> Mann.		"
<u>Adalia bipunctata</u> L.		"
EPILACHNINAE		
<u>Epilachna indica</u> Muls.		Pradhan 1935
RHIPIPHORIDAE	S R	Balduf 1969
RHIPIPHORINAE		
<u>Rhipiphorus smithi</u>	S R	Linsley <u>et al</u> 1952
RHIPIDIINAE		
<u>Rhipidius</u> spp.		Besuchet 1956
TENEBRIONIDAE		
PIMELINAE		
<u>Pimelia sardia</u> Sol.	S R	Dzimirski 1963
DIAPERINAE		
<u>Bolitotherus cornutus</u> Panz.	S ² ° R	Liles 1956
TENEBRIONINAE		
BLAPTINI		
<u>Blaps mortisaga</u> L.	R	Altevogt 1958
<u>B. pinguis</u> All.	R	"
<u>B. requieni</u> Sol.	R	"
ELEODINI		
<u>Eleodes connexa</u> Lec.	S ² ° R	Haverfield 1965
<u>E. hispilabris</u> Say	S ² ° R	"
TRIBOLINI		
<u>Tribolium castaneum</u> Herbst	R	Wojcik 1969 a & b
<u>T. confusum</u> Jacqu.	S R	Stanley & Grundmann 1965, Wojcik 1969a & b
TENEBRIONINI		
<u>Tenebrio molitor</u> L.	S ² ° R	Doyen 1966, August 1971, Gerber 1973
<u>T. obscurus</u> F.	S R	Wojcik 1969 a & b

ALLECULINAE

Androchirus erythropus Kirby

Campbell 1966

A. femoralis Ol.

2°

"

MELOIDAE

MELOINAE

C

MELOINI

Meloe augusticollis

Pinto 1972a

M. campanicollis

"

M. dianella

"

M. impressus Kirby

SI

P. 1972b

M. strigulosus Mann.

SI

"

LYTTINI

PYROTINA

Pyrota spp.

CS I

Selander 1964

EUPOMPHINA

Phodaga spp.

Pinto 1972b & c

P. alticeps Lec.

S

Pinto 1972b

Negalius spp.

S

"

Cordylospasta spp.

"

Tegrodera aloga Skinner

S

Pinto 1975

T. erosa Lec.

S

"

T. erosa var. latecincta
Horn

S

"

Cysteodemus armatus Lec.

Pinto 1977

C. wislizeni Lec.

"

Megetra cancellata Brandt
& Er.

S2°

Selander 1965

M. punctata

S2°

"

M. vittata Lec.

S2°

"

LYTTINA

<u>Lytta cyanipennis</u> Lec.		Selander 1960
<u>L. nuttali</u> Say	CS	Gerber & Church 1973
<u>L. variabilis</u> Dug.		Selander 1960
<u>L. vesicatoria</u> L.	S2 ^o R	Selander 1960, Matthes 1972
<u>L. vulnerata</u> Lec.	S2 ^o	Gupta 1966

CERCOMINA

<u>Cerocoma schaefferi</u> L.	SR	Matthes 1970
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EPICAUTINA

<u>Pleuropompha</u> spp.	C2 ^o I	Pinto 1973
<u>Linsleya compressicornis</u> Horn		Pinto 1974
<u>L. convexa</u> Lec.	CR	Selander & Pinto 1967
<u>Epicauta aethiops</u> Latr.	SI	Selander 1964, Rayah 1973
<u>E. conferta</u>	SI	Rayah 1973
<u>E. immaculata</u>	SI	"

NEMOGNATHINAE

<u>Horia minutipennis</u> Riley	C	Balduf 1969
<u>Apalus muralis</u> Forst.		"
<u>Zonitis</u> spp.		"

CERAMBYCIDAE

PRIONINAE

<u>Priomus coriarius</u> L.	S	Duffy 1946
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SPONDYLINAE

<u>Spondilis buprestoides</u> L.		Butovitsch 1939
----------------------------------	--	-----------------

ASEMINAE

<u>Asemum striatum</u> L.		Michelsen 1966
<u>Tetropium castaneum</u> L.		"
<u>T. fuscum</u> F.		Butovitsch 1939
<u>T. gabrieli</u> Weise		"

LEPTURINAE

<u>Rhagium bifasciatum</u> F.	I	Michelsen 1963
<u>R. inquisitor</u> L.		Butovitsch 1939 Michelsen 1963
<u>R. mordax</u> Deg.	R	Michelsen 1963, 1966
<u>Acmaeops collaris</u> L.		Michelsen 1963
<u>Gaurotes virginea</u>		"
<u>Stenocorus meridianus</u> L.		"
<u>Judolia cerambyciformis</u> Schrank		"
<u>Strangalia</u> spp.		Funke 1957
<u>S. bifasciatum</u> F.		Michelsen 1966
<u>S. attenuata</u> L.		Michelsen 1963
<u>S. maculata</u> Poda		"
<u>S. melanura</u> L.	S	Butovitsch 1939, Funke 1957, Michelsen 1963
<u>Leptura maculicornis</u> Deg.		Michelsen 1963
<u>L. rubra</u> L.		Butovitsch 1939, Michelsen 1963
<u>L. sanguinolenta</u> L.		Michelsen 1963
<u>L. sexguttata</u> F.		"
<u>Alosterna tabacicolor</u> Deg.		"

CERAMBYCINAE

R

<u>Neocompsa textilis</u> var. <u>alacris</u> Bates	S	Chemsak 1966
<u>Plaglanotus floralis</u> Pall.		"

METHIINI

<u>Aromia moschata</u> L.	S	Duffy 1949
<u>Oeme costata</u> Lec.		Chemsak 1965

CERAMBYCINI

<u>Cerambyx cerdo</u> L.		Butovitsch 1939, Funke 1957
<u>Hoplocerambyx spinicornis</u> Newm.		Butovitsch 1939

HESPEROPHANINI

Hesperophanes griseus F.Butovitsch 1939,
Funke 1957Hylotrupes bajalus L.

"

Penichroa fasciata Steph.

Puppin 1973

Stromatium fulvum Villiers

Butovitsch 1939

CLYTINI

Clytus arietis L.

CS

Michelsen 1966

C. mysticus

CS

"

Xylotrechus nauticus Mann.

S

Chemsak 1963

X. rusticus L.

SR

Butovitsch 1939,
Funke 1957

PURPURICENINI

Tragidion armatum Lec.

S

Chemsak & Powell 1966

Crossidius spp.

Penrose 1973

LAMIINAE

POGONCHERINI

Pogoncherus hispidus L.

Funke 1957

ACANTHOCININI

Dectes sayi Dillon & Dillon

Piper 1978

SAPERDINI

Saperda calcarata Say

Garland & Worden 1969

S. candida F.

R

Butovitsch 1939

S. populnea L.

Funke 1957

PHYTOECINI

Phytoecia spp.

Funke 1957

P. nigricornis F.

"

Oberea spp.

"

O. oculata L.

"

O. erythrocephala Schrank

"

TETRAOPINI

Tetrops praeusta L.

Funke 1957

Mallosia spp.

"

BRUCHIDAE

BRUCHINAE

Callosobruchus analis F.

Arora & Pajni 1957

Bruchidius incarnatus Boh.El-Kifl & Metwally
1971Merobruchus spp.

Johnson 1967

Stator spp.

"

CHRYSOMELIDAE

DONACIINAE

Donacia aquatica L.

S

Michelsen 1966

Diabrotica sp.

Rogers 1977

Podagrica orbiculata Motsch.

Rawat & Singh 1971

CRIOCERINAE

Liliocerus lilii Scop.

S

Michelsen 1966

Oulema melanopa L.

Merino 1969

O. melanopa ab philadelphica L.

"

CHRYSOMELINAE

Polyspila spiraeae Say

Mullins 1976

CASSIDINAE

Cassida guttata

Barrows 1979

Metriona bicolor F.

" "

CLYTRINAE

Cryptocephalus confluens Say

Tilden 1949

GALERUCINAE

GALERUCINI

Ophraella notulata F.

Welch 1978

<u>Galerucella birmanica</u> Jacqu.	R	Khatib 1934
LUPERINI		
<u>Aulacophora foveicollis</u> Luc.		Mukerjee & Chaudhuri 1960
HALTICINAE		
<u>Agasicles</u> spp.	S	Maddox 1968
ATTELABIDAE		
RHYNCHITINAE		
<u>Rhynchites cupreus</u> L.		Jancke 1934
SCOLYTIDAE		
PLATYPODINAE		
<u>Doliopygus eximus</u>	C	Jover 1952
HYLESTINAE		
HYLASTINI		
<u>Hylastes rugipennis</u> Mann.	CS	Oester <u>et al</u> 1978
HYLURGINI		
<u>Dendroctonus frontalis</u> Zimm.		Yu & Tsao 1967
<u>D. micans</u> Kugel		Francke - Grossmann 1950
<u>D. monticolae</u> Hopk.	R	Reid 1958
<u>D. ponderosae</u> Hopk.	CSR	Ryker & Rudinsky 1976
<u>D. pseudotsugae</u> Hopk.	CS	Rudinsky & Ryker 1976
SCOLYTINAE		
SCOLYTINI		
<u>Eccoptogaster ventralis</u> Lec.		Ashraf & Berryman 1969
<u>E. multistriatus</u> Marsh	CSR	Bartels 1974
<u>E. quadrispinosus</u> Say	S	Goeden & Norris 1965
XYLOTERINI		
<u>Xyloterus lineatum</u> Ol.		Fockler & Borden 1972

IPINI

Ips chalcographus Payk. Ol.

I. calligraphus Germar

C

Wilkinson et al 1967

I. confusus Lec.

"

I. paraconfusus

Schmitz, 1972

I. pini Say

"

BRENTHIDAE

BRENTHINAE

Brenthus anchorago L.

S

Malkin 1949

RHYNCOPHORIDAE

RHYNCOPHORINAE

RHYNCOPHORINI

Rhyncophorus palmarium Voss

Hagley 1965

SITOPHILINI

Sitophilus granarius L.

SR

Wojcik 1969a & b

CURCULIONIDAE

PACHYRHYNCHINAE

Pantorhytes szentivanyi Marsh.

SR

Hassan 1965

OTIORHYNCHINAE

Diaprepes abbreviatus L.

Woodruff 1968

Phyllobius artemisiae Desbr.

Thompson pers.comm.

P. pyri L.

"

RHYTIRRHINAE

Rhytirrhinus sureoufi Peyerimh.

Dumont 1920

HYPERINAE

Hypera postica Gyll.

Lecato & Pienkowski
1970

CLEONINAE

Microlarinus lareynii Jacqu.

CS

Kirkland & Goeden
1978

Stephanophorus punctiventris

Germ.

S

Eichler 1951

ERIRHINAE

Grypus equiseti F. Cawthra 1957

Pachytychius elongatus Gyll. CS Risbec 1947

ANTHONOMINAE

Anthonomus grandis Boh. SR Mayer & Brazzel 1963,
Cross & Mitchell 1966,
Fernandez 1972,
Cross 1973.

CURCULIONINAE

Curculio caryae Horn Bissell 1937

HYLOBINAE

Hylobius abietis L. CR Selander & Jansson
1977

PISSODINAE

Pissodes fasciatus Lec. Deyrup 1978

CRYPTORRHYNCHINAE

Conotrochelus brevisetis Champ. Sharp 1920

C. nemuphor Herbst C Mampe & Neunzig 1966,
Johnson & Hays 1969

5.52.1 CARABIDAE

Mating behaviour has been recorded for 32 genera in three sub-families.

In the Carabidae the copulatory position is similar in all species; the male dorsal to the female, both facing in the same direction (Zikan, 1929). From studies of four species of Cicindela, (Willis, 1967), the male approaches a female in short runs, making a final quick dash and leaping onto the female dorsum. The male fastens the mandibles around the junction between the female pronotum and elytra, the fore and mid legs grip the female. Pads of adhesive setae on the underside of the first four tarsal segments are adapted for this purpose. The hind legs rest on the substrate behind the mating pair.

The male may remain mounted for a while before coupling takes place (Shelford, 1908) and similarly may remain so after copulation is over as in C. punctulata, (Goldsmith, 1916).

The female is coy, rarely copulating without a struggle or curling her abdomen ventrally to prevent insertion of the male genitalia (Mitchell, 1902). Males, however, are very persistent and the apex of the aedeagus may be used to probe the end of the female abdomen (Moore, 1906).

Once the male and female are in copula they touch and vibrate their antennae. One or several insertions of the aedeagus may be made, each insertion lasting from one to several minutes, the total mating time varying from a few minutes to several hours. No species specific elements in the mating behaviour of Cicindelinae have been recorded.

Only two species of Brachinus have been observed in copula and for B. sclopeta (a gregarious species) Wautier & Wautier (1967) only give information on seasonal mating times and degregarisation in a premating phase. In Brachinus pallidus the copulatory position is similar to species of Cicindelinae, although the hind legs of the male grip the female around the tip of the elytra. During copulation the

male "stimulates" the female by rubbing the hind legs over her elytral apices, and antennates the female antennae. After insertion of the aedeagus the small parameres at the base of the median lobe remain external. In Cicindela intromission lasts for only a few seconds after which the male may remain mounted.

According to Delkeskamp (1930), the duration of copulation in the Carabinae varies from a few seconds to several hours.

From his studies on Pterostichus Witzke(1973) suggests that carabids show little specialisation with regard to sexual activity. Nothing regarding "partner seeking" and "enticement to copulate" has been described, since it was previously supposed that in nature pairing occurred by accident. It has been noted many times that a female rarely copulates readily without a struggle. Witzke suggests there is a specific stimulus produced by the male which ends the resistance of the female.

In Asaphidion flavipes (Bauer, 1971), Pterostichus vulgaris and Harpalus pubescens (Witzke,1973) the male "stimulates" the female with his antennae. In the case of A. flavipes the male moves rapidly to the female and mounts her whilst beating the female's laterally directed antennae with his forwardly directed antennae. A lack of receptivity in the female is shown by opening of the mandibles and raising the abdominal apex.

Carabus nemoralis males palpate and antennate the female abdomen prior to mating and then rapidly climb onto the dorsum of the female from the rear. The male then strokes his spined tibiae over the female elytra which makes an audible crackling noise (Delkeskamp, 1930) whereupon female resistance, exhibited by pressing her abdomen tip into the ground, ceases. Males of C. cancellatus (Kirschner, 1927) and C. auratus (Balduf, 1969) rapidly climb onto the dorsum of the female, who raises her head in order that the mouth parts of the pair make

contact. This activity appears to be a necessary preliminary before insertion of the aedeagus. The male antennae then beat on the backwardly directed antennae of the female.

Similarly, males of Nebria complanata (King & Stabins, 1971) palpate the female head and thorax, and antennate the female antennae immediately upon mounting to "quieten" the female before moving posteriorly into the copulatory position for intromission.

The parameres in Pasimachus punctulatus and P. elongatus are slender, blade like structures bearing a comb-like row of long setae along their ventral edges near the tips. After mounting these are used to tap the apex of the female abdomen in a definite rhythm to stimulate the opening of the female genital orifice. (Alexander, 1959; and Cress, 1966). Each time the female sclerites slightly move, the median lobe is directed anteriorly, the tapping resuming if insertion is unsuccessful. The parameres appear to have no further function and remain external to the female during copulation. There are no comparisons with other species but Alexander suggests the sensory stimuli produced by the parameres may be important in species isolation. In addition in P. elongatus, prior to the extrusion of the aedeagus and subsequent stimulation by the parameres, the male hind legs alternately kick the lateral portions of the female abdominal sternites in a rapid rhythm.

While belonging to the same tribe as Pasimachus, Scarites substriatus is not known to use parameres in the same way. Instead there is some element of courtship behaviour prior to mounting where the male grasps a female with the mandibles initially at any point on the body. He then turns to face the female and seizes a mandible. While in this position the antennae of both beetles are rotated in a large arc; the male then uses his grip on the female mandible as a lever to attain the mating position. During mating the male may use the hind legs to

brush the elytra and abdominal sternites of a restless female (Hlavac, 1967). Similar sideways movement of the antennae prior to intromission has been recorded in Brosicus cephalotes (Michelsen, 1963).

According to Witzke(1973) the specific stimulus in Pterostichus niger, P. nigrita and P. cristatus is the repeated rubbing of an oblong tubercle on the male sternite VII against the female elytra. This done while the male is in the mounted position inserting the aedeagus and at the same time the male antennae vibrate briskly. Although present in a number (but not all Pterostichus species), the use of an abdominal tubercle is not noted by Larochelle (1973) in P. chalcites although he also mentions that the female rarely accepts the male without a struggle. There may be small differences in shape of the tubercle, but in closely related species the tubercle may be present in some and absent in others, and differences may occur in the way in which it is used. Witzke(1973) suggests that copulation between different species of Pterostichus is possible but regards differences in body size, structure of the copulatory organ, ecology biology (as limiting factors), and perhaps also the frequency of male movement prior to intromission.

Leitner (1943) suggests that the reproductive isolation of species of Trechus may involve species specific scents emanating from the pygidial glands. Trechus noricus and T. regularis apparently have the same odour as T. palpalis but this differs from that of T. ovatus. Leitner concludes that more refined techniques may show differences between the former three species. Trechus species inhabit dark and cryptic situations where olfaction might be supposed to be a suitable mode of communication.

Larochelle(1972a&b) gives a list of the duration and seasonal mating times for 16 genera.

5.52.2 HALIPLIDAE

Information here is provided for just one species, Haliphus wehnckeii (Beier, 1929). Observations were made in a small aquarium. There is no pursuit of the female by the male, instead the male climbs onto water plants and may mount a passing female, or the pair may meet while swimming, when the male climbs quickly onto the female dorsum. The male grips the female around the pronotum with his forelegs, around the epipleura of the elytra with his mid-legs, whilst the hind legs are held free behind. The fore and mid legs bear patches of adhesive setae on their undersides which are adapted for clinging to the female. When the male is mounted on the female dorsum he stridulates, with accompanying movements of the hind legs and abdomen. This "stimulates" the female to allow copulation to take place. The duration of copulation varies between 2-30 minutes. The male may remain mounted on the female for some time after copulation. Stridulation is repeated intermittently.

5.52.3 DYTISCIDAE

Information on mating behaviour in the Dytiscidae is available for four genera. Scheidt (1909) and Brocher (1926) give only seasonal times of mating for Dytiscus species.

In three species of Rhantus, R. gutticellus, R. binotatus and R. atricolor, courtship is simple without readily observable differences between species (Smith, 1973). Specific and sexual recognition is thought to be olfactory since previously isolated males and females locate each other and copulate placed together in total darkness. Recognition is followed by rapid movements by the male who attempts to clasp the female. If this is unsuccessful, a courtship chase is initiated where the male follows the female in an erratic circular or spiral swimming pattern. Claspings is accomplished when the male

hooks the pro and meso-tarsal claws on the underside of the female prothorax, using adhesive setae on the expanded tarsal pads. The female is resistant until the male attains a secure grip, whereupon she becomes quiescent. It is thought that the female resistance is a form of mechanical isolation since the female venter and male fore-tarsal claws have co-evolved so that only conspecific clasping is achieved. The claws differ dramatically between species in the genus Rhantus. Acoustic signals are produced by R. gutticollis and R. binotatus but these are exclusively associated with emigration.

Males in the tribes Colymbetini, Dytiscini and Cybistrini all have highly modified tarsi used for adhesion to the female during coupling.

Balduf (1969) reviews the behavioural studies of Blunck (1912a,b&c) on Dystiscus marginalis. As in Rhantus, acoustic signals are produced during mating. Olfactory cues are thought to be involved. After recognition mating may be delayed in D. marginalis and the male may pursue a female, with a courtship display by the male which includes "shaking" his body, making drumming noises and striking the female head with his antennae and mouthparts.

The copulatory position is similar in all observed species of Dytiscidae and like that found in the Halipilidae.

5.52.4 GYRINIDAE

Although Hatch (1925) and Balduf (1969) review mating behaviour in three general of the Gyrinidae they do not present any information on sexual recognition (the male moves rapidly to the female) or behaviour during copulation. Males of Gyrinus substriatus bear an adhesive organ on the anterior tarsi for clinging to the female elytra.

In both Dytiscidae and Gyrinidae the lateral lobes of the aedeagus do not enter the female during copulation; they appear to function in the passage of the spermatophore from the male to the female.

5.52.5 SILPHIDAE

There is information on mating behaviour in three genera.

In Necrodes and Nicrophorus sexual contact is accidental, as part of the search for food, since the species are gregarious at vertebrate carcasses.

There is little sexual dimorphism in Necrodes surinamensis and sexual recognition is thought to be by "direct contact" (Ratcliffe, 1972). The males and females touch maxillary palps but this does not always lead to copulation. The role of pheromones, tactile and visual stimuli in aiding the recognition of a mate is unknown. The male may pursue a female before mounting, whereupon the female may exhibit resistance. Upon mounting, the male "stimulates" the female by rubbing his maxillary palps against the female pronotum whilst pulling back the female antennae with his mandibles. Prior to insertion, the genitalia may probe the female abdomen tip.

Balduf (1969) discusses the production of a sex attractant by male Nicrophorus. The male climbs to a high place on the carcass and rests with his mandibles touching the substrate and the abdomen elevated. Usually only one pair of beetles is associated with a carcass and copulation takes place regularly in the course of burying. This is accompanied by acoustic signals produced alternately by the male and female which are thought to express receptivity.

5.52.6 STAPHYLINIDAE

Information on mating behaviour in the Staphylinidae prior to this study is very limited; only 14 genera have been observed and these in varying detail. Frank (1968) merely gives seasonal information on mating in various Quedius species, and Smith et al (1978) assume above ground mating in the fossorial Osorius planifrons.

Owing to the diversity of mating positions, secondary sexual

characters, and recognition signals used in the Staphylinidae, each sub-family in which information on mating behaviour is available, will be considered in turn.

1. Omaliinae

Males of Eusphalerum spp. were observed by Blum (1976) to stand stationary and rotate their antennae. Then on meeting the female the male would briefly antennate her before mounting. A pheromone is thought to be involved since a male would relentlessly pursue a female until copulation was achieved. Scheerpeltz (1929) detected small white vesicles in the genital region of Olaphrum which he interpreted as scent glands.

Although Steel (1960) stated that most omaliines do not exhibit genitalic differences, in some species differences are seen in the median lobe apex, lateral lobe shape, the posterior margins of sternite VII and teeth on the posterior trochanters in males (Section 4) of closely related sympatric species.

2. Tachyporinae

Lipkow (1966), studying Tachinus and Tachyporus spp., observed that the male seeks and mounts the female from behind, the female often offering resistance. During coupling the male continues to grip the female pronotum with the fore legs.

During copulation of Tachinus signatus the male vibrates his antennae, then just prior to termination the female walks slowly away, the male "falls" to one side and the genitalia are disengaged (Section 5.2.14).

No mention is made of the wealth of secondary sexual characters in Tachinus (Section 4.3.6), the arrangement of peg setae of sternite VII (propygidium) in the male, and the elaborate lobes on sternite and tergite VIII (pygidium) which differ in both sexes. During observations on species of Tachinus, in the present study, the precise function of

the secondary sexual features was not determined. However, bearing in mind the striking differences between some sympatric species and the direct evidence that such structures come into contact with the opposite sex during mating, a role in species specific tactile signalling must be considered probable. The aedeagus is of rather constant form in Tachinus, but does exhibit small specific differences.

Other species of Tachyporinae have good secondary sexual characters, although these are not as elaborate as those of Tachinus and closely related genera. In some Mycetoporus and Bolitobius species the males have lobes and groups of setae on the ventral side of the abdomen which are specifically distinct, but differences in aedeagus morphology are very slight.

3. Aleocharinae

The majority of observations have been made on aleocharine genera, Lomechusa, Atemeles, Myrmedonia, Dinarda, Velleius and Aleochara, which do not exhibit the typical staphylinid copulatory position.

Kemner (1926), Voris (1934), Baldur (1969), Colhoun (1953) Fuldner (1960), Welch (1964), Blum (1976) and Peschke (1978a & 1978b) have described mating behaviour in Aleochara spp., A. curtula mainly.

A male A. curtula raises the abdominal apex dorsally over his own head extrudes the genitalia and, while the female is still or otherwise preoccupied, attempts to clasp the female abdomen tip with the parameres. The parameres slide over the apex and eventually grip, laterally, the sclerites of the ninth segment. If the female is receptive the male immediately obtains a firm hold. Only when the male is rejected does he pursue the female with his head close to the female abdomen apex.

According to Peschke (1978a), the contact and orientation of the male on the female abdomen is possible owing to the extremely differentiated flexibility of the parameres as sensory and grasping organs with their associated complex musculature and articulated joints. The

parameres are probably rotated and placed with their medial surfaces on the female tergite VIII. This arrangement may allow the male to tap the abdomen of the female to evoke exposure of the vulva. This may also provide adhesion between the aedeagus and female abdomen. The apical lobe of the paramerite, which has strong musculature, may be moved to tap the female, the broad expanse of the medial surface may provide an adhesive surface. Dermal glands may provide a secretion to facilitate adhesion (Seevers, 1978).

Peschke (1978b) investigated the production of a sex pheromone in female A. curtula which triggers the reaction of grasping by the male parameres. This is the first record of a female sex pheromone in the Staphylinidae. Visual, gustatory and mechanical stimuli are excluded as having any function in recognition or isolation. The production of a sex pheromone was indicated from the response of males to hexane extracts of females on wax models. The pheromone is thought to be spread all over the body and perhaps trapped in the epicuticular waxes. Grasping of the parameres was triggered by freshly killed females before contact was made with the antennae. Once the parameres grip the female the median lobe is inserted several times, each insertion lasting a few seconds.

There is complex morphological co-adaptation of the male and female genital organs; in particular the composition of the internal sac with its flagellum and the hook on the male median lobe, which is fixed between the genital chamber plate onto a hook-like sclerite in the female. Examination of closely related species has shown that these structures could act to prevent inter-specific insemination.

Other aleocharines; Lomechusa strumosa, L. emarginata, L. paradoxa Myrmedonia, Dinarda and Velleius dilatatus on which there is only limited information mate in the same position which is only possible owing to the great flexibility of the abdomen. Outside this family

this type of copulation is only known in Sialis flavilatera (Megaloptera).

Keys (1914) reports that during copulation in Lomechusa paradoxa the female may direct her antennae back over her body and stroke the up-curved abdomen of the male. Prior to copulation in L. strumosa the male and female touch their antennae and mouths together, tapping each other quickly, after which the male moves to the abdomen tip of the female touching her constantly with his antennae (Balduf, 1969).

Apart from striking differences in the genitalia of closely related species, differences also occur in the female spermatheca which is heavily sclerotised. In some genera the male tergite VIII and sometimes tergite VII are variously modified, the hind border with different shaped lobes and the surface of the sclerites with variously positioned protrusions: e.g. Gyrophaena, (Section 4.3.7).

Most aleocharines mate in the position where the male abdomen is upturned over the head, except for the more primitive Gymnusa and Deinopsis which are thought to mate in the normal dorsal riding position. Some other genera where the abdomen has become shortened and thickened have reverted to the dorsal position. The mating behaviour of Cypha longicornis is described (Section 5.2.15). The mating position in this species is thought to be secondarily derived from the usual aleocharine position owing to the shape of the abdomen.

It is, however, significant that in many genera which exhibit the secondarily acquired mating position, the male secondary sexual characters are dorsally positioned on the abdomen and would come into contact with female receptors during coupling (Section 4.3.7).

Oxytelinae

In many genera there are differences in the genitalia between closely related sympatric species. In Thinobius spp. there are substantial differences in the structure of the median lobe apex.

Platystethus spp. have minor secondary sexual characters, but lobing on the posterior border of the male sternite VII show constant differences between species, along with minor differences in the shape of the lateral lobe. Substantial differences in the genitalia are seen in Carpelimus and also in Anotylus, where the male sternite VIII is very characteristic for each species. Here the females of different species are almost indistinguishable.

5. Steninae

Michelsen (1963) observed stimulatory movements of the male antennae of Stenus spp., where the male makes single rhythmical strokes over the female, possibly hitting her eyes with each stroke. Then during copulation the male grasps the female antennae between his mandibles.

In the Steninae secondary sexual characters are generally poor, although there are good genitalic differences, particularly in the apex of the median lobe and in the breadth of the spatulate tip of the lateral lobe (Section 4.2.4). In addition males of Stenus providus and S. clavicornis have distinct patterns of ventral pubescence on the abdomen (Section 4.2.3).

6. Paederinae

Although Rugilus spp. are without obvious secondary sexual characters, Lathrobium, Lithocharis, Medon and Scopaeus show striking differences in the male abdominal sternites and the very elaborate apical structures on the genitalia. In Lathrobium the armature of the internal sac is often distinct in closely related sympatric species (Section 4.3.4). Mating behaviour in Rugilus orbiculatus is described (Section 5.2.10).

7. Staphylininae

Mating behaviour in the main tribes of the Staphylininae is discussed.

Othiini

Nothing is known from the literature of the mating behaviour in the Othiini.

Mating behaviour of Othius myrmecophilus is described (5.2.11).

Xantholinini

Nothing is known from the literature of mating behaviour in the Xantholinini. Xantholinini spp. show considerable differences in the armature of the internal sac. Mating behaviour in Gyrophypnus fracticornis is described (Section 5.2.12).

Staphylinini

Nield (1976) discusses mating in Staphylinus olens where there is no pair interaction at distances greater than 5 cm. Normal encounters between a pair involve face to face confrontation followed by a struggle. Encounters which lead to mating attempts always commence with an approach by the male from behind the female. Contact with the female often results in raising her abdominal apex which makes mounting by the male difficult. The male approach is highly characteristic consisting of a series of short darting movements superimposed on the normal walking rhythm. Apart from aggressive behaviour the female is passive. The initial mounting position is dorsal, with the male moving secondly to one side and then assuming an end to end position with female.

Blum (1976) refers to the succession of positions in S. olens (i.e. dorsal riding - V-shaped falling to one side - end to end) as an evolutionary trend in the Staphylinini. End to end copulation is thought to be an adaptation to the burrowing and crevice living habit.

Mating behaviour in Creophilus maxillosus is described by Fichter (1949). Kramer (1955) states that virgin adults copulate within 24 hours after emergence. Copulation is preceded by reciprocal antennal fencing and palpation in the face to face position. This is followed by antennation and palpation of each others abdominal apex. The female may show resistance to mounting. The male mounts and copulates in the dorsal riding position with his expanded fore-tarsal segments gripping the female pronotum. Movement of the female during intromission generally forces the male into an end to end position. A male may attempt to copulate with an already engaged female, which results in male to male conflict and often causes the disengagement of the copulating pair. In cages males attempted to mount females each time physical contact was made.

Quediini

There is no information in the literature on mating behaviour in the Quediini. The secondary sexual characters of the Quediini are discussed (Section 4.3.5) and mating behaviour in species of Quedius is described (Sections 5.2.8 and 5.2.9).

Philonthini

There is no information in the literature on mating behaviour in the Philonthini. The secondary sexual characters of the Philonthini are discussed (Section 4.3.5) and mating behaviour in nine species of Philonthus is described (Sections 5.2.1 - 5.2.7).

5.52.7 HYDROPHILIDAE

Stress chirps were analysed in 12 species of Berosus by Van Tassel (1965). Sympatric species were shown to have comparatively different chirps, whilst allopatric species were not always easy to distinguish. An analysis of premating sounds in 4 species exhibited marked inter-specific differences, differing in the timing of chirps. This was

clearly associated with courtship, preceding, but not continuing during or after, copulation. It was therefore concluded that this acts as an important reproductive barrier.

Balduf (1969) reports that male stridulation occurs in Hydrobius fuscipes and Spercheus emarginatus, where a peg on the side of the abdomen is rubbed against the elytra. During copulation a male Hydrobius fuscipes lowers his head over that of the female, drums on her labrum with his palpi and may also stridulate faintly.

Suckers on the male fore tarsus of Hydrous triangularis, similar to those found in the Dytiscidae, are probably used to cling to the female during copulation.

In Helophorus, morphological differences between species are slight and are virtually confined to features of the aedeagus. From observations of courtship and mating, little was observed regarding reproductive barriers. Experiments on hybridisation illustrated the operation of both pre and post-mating barriers. Unmated females laid eggs in the presence of males belonging to different species, and when hybrids were produced they were sterile (Angus, 1970).

5.52.8 HISTERIDAE

Very little is recorded on the biology of histerids. Lierath (1955) reports courtship processions of Hister fimetarius on sunny days which consist of a female and several males. The female leads the procession with a male on both sides, each grasping a mid leg with their mandibles. Then a succession of males follow behind, each male clasping a leg of the male in front. The female struggles, and the strongest male attacks his rivals whilst keeping hold of the female. This male then uses the mid leg as a lever and support for mounting the female's smooth dorsum to copulate.

5.52.9 HELODIDAE

Nyholm (1969, 1972a, 1972b) discusses the morphology and mating behaviour in Cyphon coarctatus. Closely related pairs of species often have different habits or habitats; however, where sympatric pairs do occur structural differences are present. Such differences are found in the apex of the male genitalia, and in the female in the prehensor (the strongly sclerotised armature of the bursa copulatrix) which grips the spermatophore.

During mating the male "tastes" specialised hairs on the female elytra where secretions are produced. This is thought to be of great importance for sexual activity, and releases a further stage of mating behaviour in the male.

5.52.10 LUCANIDAE

Information on mating behaviour exists for species of 4 genera. Three species of Lucanus have been observed by Brull (1952) and Mathieu (1969).

In Lucanus cervus, on humid days in June, when the males are active and flying an experiment was carried out in an enclosure using a block of wood (Brull, 1952). Around the circumference of the block the female emitted a secretion from her anal opening. This secretion excited males in the vicinity who were immediately attracted to the block, several males being knocked off by one already there. This male rotated around the secretion and touched the female anal opening with his antennae and maxillary palps. Dorsal mounting and copulation followed with the male gripping the female with his mandibles. After the first copulation the male was pushed away while the female continued to emit the secretion and copulation was repeated.

Such a secretion is not noted for other Lucanus species, although

Mathieu (1969) believes that sex recognition is chemotactic at close range.

In L. capreolus after recognition the male pursues the female with his mandibles projected forward, whilst in L. placidus this does not occur. Before insertion of the genitalia the male performs mandible pressing, which involves their forward motion whilst rubbing and pressing the sides of the rounded pronotum of the female. This action produces an audible noise. During intromission the asymmetrical sharp edged lateral lobes are placed in front of the female genital pore, above the fifth visible sternite.

Multiple mountings and copulations by the same male is the rule, a mounted male may overpower a female so that 8-10 matings may be performed without a struggle.

After sex recognition in Dorcus parallelus the male, with his mandibles open, pursues the female whilst constantly palpating and vibrating his antennae over the female. When mounting, the male bites the striated female elytra which, as in Lucanus, produces a characteristic sound.

Similar sound production also occurs in Platycerus virescens, where the male rubs his mandibles over the female pronotum for periods of about 10 minutes. The male also moves his head over the pronotum whilst rubbing the surface with his palps and touching each side of the female head alternately with his antennae. During insertion of the genitalia the male may rub the tip of the female abdomen with the hind legs and then uses the sharp edge of the lateral lobes to pull the last visible sternites of the female upward.

In Ceruchus piceus male palpal and antennal activity is triggered upon encounter with a female. Prior to insertion of the genitalia the aedeagus may be rubbed over the dorsal side of the female abdomen. During copulation the mid legs may rub the elytral striae and the

hind legs rub the abdominal apex of the female.

In males of Lucanus and Dorcus the mandibles are long and used for "subdueing" and maintaining the female in position during mating. In contrast, in males of Platycerus and Ceruchus the shorter mandibles are not used for holding the female, instead the legs are rubbed intermittantly against the female elytra.

5.5.2.11 PASSALIDAE

Schuster (1975) has observed copulation in 6 species belonging to 2 genera, and records some new mating positions for beetles. The general mating behaviour is similar in all species. Courtship begins with mild aggression by the male and the production of an accoustic signal. The male circles a female for up to 12 hours; eventually the male and female position themselves so that contact is venter to venter, followed by rotation in the horizontal plane until the abdomen tips brush across each other with the genital pores opposed. Once the aedeagus is inserted the male ceases the accoustic signal. After a quiet period both beetles become active and move their legs. Copulation is terminated by the female walking away. After copulation the male makes a few loud sounds and is very active. This is followed by post copulatory signals of low intensity.

The new mating positions recorded include:

Odontotaenius disjunctus and O. zodiacus; venter to venter, (male venter up) followed by end to end.

O. striatopunctatus; venter to venter (male dorsum up) followed by end to end.

Passalus (Passalus) punctiger; venter to venter (female dorsum up) 30° apart in rotation, male aedeagus twisted 180°. To separate the female rotates to 90° and the male becomes dorsum up. P. (Pertinax) affinis; similar to P. punctiger although the female remains dorsum up. P. (Pertinax) convexus; 90° position (female dorsum up).

At the end of copulation 180° position and male dorsum up.

The only other beetles known to have an inverted end to end position are the scolytids, Dendroctonus and Pityogenes.

In insects in general, inverted end to end mating occurs in a few Diptera, Homoptera, Tettigonoidea, Blattodea, and Dermaptera. In the end to end position the aedeagus is untwisted, and there is a selective advantage for males which are able to twist the aedeagus so that intromission can occur without rotation, and contact is not lost between the sexes. If contact is broken the whole sequence of courtship stimulation may have to begin again. At 30° rotation, or less, the pair would remain in antennal contact whereby stimulation and other communication is possible.

5.5.2.12 SCARABAEIDAE

Information on mating behaviour is available for 32 genera. Halffter & Matthews (1966) give information on the biology of several species in the Scarabaeinae. In this sub-family sexual encounters occur at the food source or in relation with brood ball-forming, by what appears to be accidental contact. The search for the opposite sex is therefore an indistinguishable part of the search for food;

however, it is common for the beetles to congregate at only a few food sources.

In the Scarabaeini it is thought that sex recognition cannot occur without direct contact or very close approach. This is achieved by head to head contact with the antennae and maxillary palps and is therefore likely to be of chemotactic nature.

If a ball has already been formed, and the beetles are of the same sex, hostile combat follows contact. If they are of opposite sex, and not already attached to a partner, there will be immediate acceptance and formation of a partnership. This occurs in Scarabaeus, Gymnopleurus, and Sisyphus, while in two species of Canthon there will be a brief combat (lasting a few seconds) before the female will be accepted by the male.

Formation of pair bonds is detailed for Copris hispanus, Phanaeus nimrod, Scarabaeus and Dichotomius carolinus (Halffter & Matthews, 1966).

There is no courtship of the ritualistic kind in the Scarabaeinae. It seems that the prolonged co-operation in nidification serves the same purpose since it brings the two members of the pair into repeated contact before copulation takes place.

Unlike the Scarabaeni, Phanaeus (tribe Coprini) does not copulate after brood ball construction and rolling (Halffter & Lopez, 1977). The initial stimulus is the approach to the female by the male, followed by her detainment. Then, following a positive response from the female indicating her receptivity, the male mounts drumming rapidly on her pronotum and anterior part of the elytra with his front legs. The lateral lobes are engaged in the genital opening and insertion of the median lobe follows.

In the Aphodiinae Schmidt (1935) observed three species of Aphodius in which mating behaviour is very similar. The female assists

the male during mounting by keeping still. Most Aphodius species mate on the surface of, or in, dung.

Rutelinae species mate on the ground surface or on flowers. Cotalpa puncticollis lives on Juniper. Owing to a colour dimorphism, the males seek out females visually and mating takes place amongst the foliage. There is no elaborate pre-mating behaviour. (Cheary et al, 1972). In Cotalpha granicollis the female is approached from behind and mating is accomplished after her head is forced down, and her abdomen raised by the male hind legs. Mating here takes place at the female's burrow, or on the surface of the ground (Jorgensen, 1963). Pilleri (1966) merely records the mating time of Anisoplia tempestiva, where the females fly to the male using either visual or olfactory cues. Ladd (1970) and Barrows&Gordh(1978) record sex pheromone production of abdominal origin in unmated female Popillia japonica. Males attempt to copulate with females as they emerge from the ground, or on their host plants. The female sex attractants appear to attract only males, while the males produce a pheromone which attracts both sexes, probably for aggregation. Males fly near vegetation searching for females and land when a female is located to mount and copulate. There is no conspicuous courtship prior to mating; however, the male may remain mounted after copulation and sequences of post-copulatory behaviour may last over two hours. Such behaviour includes, head nodding, male antennation of female, male hind legs rubbing the female abdomen and may be associated with sperm competition. Female P. japonica cease to produce sex attractants after they have mated.

Milne (1960) and Rittershaus (1927) suggest that sex recognition is probably at close quarters in Phyllopertha horticola. The olfactorial ability is not so well developed as in other Lamellicorns and a male may only detect a female from a very short distance (5-10 cm) downwind. Recognition is generally achieved after brief

tactile examination. Pairing depends mainly on chance physical encounters, whereupon copulation follows immediately.

Schmidt (1915) recorded swarming on consecutive days at the same hour as being associated with copulation. Copulation in Anomala aenea is similar to Phyllopertha.

The Melolonthinae mate on vegetation or on flowers, some species during the day and some at night. Landa (1960) only records duration of copulation for Melolontha melolontha.

Weber (1915) describes copulation in Melolontha vulgaris, which occurs in the morning and evening. The male climbs onto the female dorsum and vibrates his clubbed antennae. Once in the mounted position the male strokes the female hind abdomen with his hind tarsi, the lateral lobes are spread out over the female genital orifice and the median lobe is inserted.

In the rosechafer, Macrodactylis subspinosus syriaca, mating aggregations occur on milkweed plants. The males are probably attracted by sex pheromones produced by the females (Bennett, 1974). When a pair come into contact the male quickly mounts and grasps the female, with his fore-legs, between the thorax and abdomen. Just prior to insertion of the aedeagus the male makes several quick vibrations of his body. Following mounting and during copulation the male scrapes the female pronotum with his mandibles leaving a shiny longitudinal line amongst the pubescence (Halffter & Lopez, 1977). The response of the female to this is to remain quiet, raising her abdomen and separating the pygidium from the other abdominal sternites. Male homosexual behaviour has been observed.

A sex attractant is also produced from a milk-coloured gland at the end of the abdomen in virgin females of Rhizotrogus aequinoctialis. After mating the females are not attractive any longer, although the males are polygamous. The attractant acts in the range of 200 m.

Amphimallon majalis (Menees, 1963) and A. assimilis (Rittershaus, 1927) are reported to differ from one another in their method of sex recognition. Rittershaus suggests that a male A. assimilis only detects a female when he accidentally comes into contact with her. The male perceives the female sex through olfactory means by waving his antennae over her hind abdomen. The female may make defensive movements with her hind legs when the male attempts to mount. The male first mounts the female and climbs well forward so that his head is positioned over that of the female and stimulates her with gentle, fast antennal strokes. To copulate, the male must move posteriorly, raising his head and thorax upwards and curls his abdomen ventrally until the genital orifices are opposed.

In contrast Menees (1963) suggests that A. majalis swarm in the evening, around trees, for 25-30 minutes during which time the female is thought to give off an attractant pheromone. At the end of swarming copulation takes place. In the field up to 7 males may attempt to mate with a single female. No courtship was observed before mating. On approaching a female, the male becomes highly "excited" and moves about with his lamellate antennae opening and closing.

Ritcher (1958) gives the mating sites for 7 genera of Dynastinae, as being in soil, on the ground surface, on flowers, in termite galleries or in stumps of fallen trees.

Dale (1963) in describing the mating behaviour of Pericoptus truncatus, says that flight is not a necessary prelude to mating, but gives no information on courtship and recognition.

Beebe (1944) noted that Megasoma elephas are stimulated to mate after being drenched with water. There seems to be no preliminary courtship and no opportunity for appraisal of the male horns by the female.

Trichotinus piger and T. assimilis display similar mating behaviour which differs only in the duration of copulation (Hoffman, 1935). Copulation takes place during the day on flowers. After mounting, and prior to insertion of the genitalia, the male rapidly strokes the pronotum of the female with his maxillary palps and gradually extends the genitalia. The distal end of the clasper is used as a wedge to open the pygidium of the female enough to allow insertion of the aedeagus. After this the clasper is used to keep the genital plates spread during copulation by clamping onto the female. If the female kicks with her hind legs so that the clasper becomes loosened, copulation is usually terminated.

The Geotrupinae burrow in soil and copulate there. In Geotrupes mutator copulation is started by courtship, where the male approaches the female from behind striking her over the elytra with his fore-legs as she rotates. The male then attempts to mount the female. During the mating season a female produces a strong sex attractant, which may attract many males (Teichert, 1955).

The female also produces a sex attractant in Pleocoma hirticollis vandykei. From observation in cages males showed immediate signs of "stimulation" upon introduction to a female, since the aedeagus was extruded and the female was then approached. The female buried her anterior half into sand and opened her vaginal orifice whereupon the male inserted the aedeagus. In addition Barrows & Gordh (1978), Ritcher (1958) and Halffter & Matthews (1966) give information on mating sites in the various sub-families.

Ritcher (1958) suggests that in the Scarabaeidae the sclerotised accessory genital processes of both males and females are so constructed that cross mating between most species is physically impossible. However, in the case of closely related species some evidence has been found that cross mating does occur and that hybrids may be produced,

e.g. Phyllophaga hirticula x P. rugosa hybrid
 Male Cyclocephala borealis x C. immaculata eggs

5.52.13 BUPRESTIDAE

Mating behaviour has been observed in 9 genera.

Beer (1970) reports rapid thumping of the abdomen against twigs of the host plant in both sexes of Chrysobothris and Polycesta abdita. There is no indication whether the thumping is in any way species-specific.

Olfactory cues, followed by tactile signals, play an important role in location and communication in male and female Hippomelas planicosta (Alcock, 1976). A pair may remain together for several hours, during which time they copulate repeatedly. The male remains on the dorsum of the female in the intervals between copulations, and strokes the female with his legs and antennae before, during and between copulations. The mid-legs stroke the female elytra and abdominal venter; the fore-legs may jerk along the side of the female thorax; the hind legs pat the posterior abdominal venter and the antennae drum on the female thorax, head or antennae. The stroking is thought to serve to elevate the "sexual motivation" of the female, eliciting copulation and preventing her premature departure.

In warm, sunny weather on pine Buprestis rustica females vibrate their antennae and produce a sound reminiscent of certain longhorn beetles. This is followed by movements which resemble a mating dance (Lejfelt & Lejfelt, 1978).

In Xenothipsis brendeli, Hesperorhipis and Trichinorhipis, the male antennae are elaborate and pectinate and the females are thought to emit a pheromone. Males are attracted to virgin females at a particular time of day and males which have been antennectomised are not attracted (Wellso, 1966).

Dutt (1969) and Carlson & Knight (1969) describe mating behaviour in species of Agrilus. Sympatric species A. horni, A. anxius and A. acutus depend on host selection to bring about meeting of the sexes, and prevent inter-specific matings. The male courting response is elicited by probing the female pygidium with the aedeagus upon mounting. The structure of the pygidium enables the male to differentiate between males and females. Prior to insertion of the aedeagus the male projects his head and prothorax forwards and vibrates the antennae over the female head and pronotum base, making some long strokes over the lateral parts of the pronotum. At the same time the male palpates the female pronotum, and this may continue during and after copulation. There is thought to be a possibility that high frequency vibrations or slight sounds, produced by some of the movements during antennation, may differ between species. Both sexes do produce other stridulatory sounds which are not species-specific and only occur in stress situations. A. horni is thought to emit air-borne sex attractants.

In laboratory conditions inter-specific copulations may be achieved.

Female A. anxius x Male A. g. liragus

Female A. acutus x Male A. horni

A. acutus were found also to be receptive to A. g. liragus and A. anxius males.

In Pseudocotalpa giulianii, the males fly to creosote bushes 1 hour before dark where females emit pheromones. The males land near to the females and mount from behind, their final location being visual. Upon mounting the male immediately strokes the prothorax and head of the female with his antennae whilst simultaneously rubbing the apex of the female elytra with his hind legs. This is followed by genital insertion (Hardy, 1976).

To support the idea of female sex pheromone production, the males of some genera have more sensory foveae on the antennae than the females. These structures are thought to function in mate recognition (Levey, 1978).

In the Buprestidae the degree of host specificity varies considerably, wood boring species tending to have wider host ranges than leaf and stem mining forms. Most adult Buprestidae frequent their larval host plants although many can be found on flowers of 'non-larval' host plants (Levey, 1977).

5.52.14 ELATERIDAE

Information is available for only 2 genera.

In Pyrophorus atlanticus the females attract males with prothoracic luminescence. In P. pellucens the males and females fly prior to mating, the female glowing and the male pursues the female to the ground where she stops glowing. Final location of the female is then achieved by olfactory means (Lloyd, 1965).

Zacharuk (1958) suggests that females of Ctenicera aeripennis destructor produce a pheromone to attract males. Mating occurs immediately after emergence, in soil cracks or under cover. When the male is attracted to the female, he strokes her pronotum vigorously with his antennae during which time the aedeagus is extruded. The lateral lobes become anchored by lateral pressure of their hooked and spinose tips, in the lateral walls of the genital pocket (vagina) in the eighth segment of the female. Unmated males are not attracted by fertilised females.

The Elateridae do not have striking secondary sexual characters.

5.52.15 EUCNEMIDAE

The only information available is for Melasis buprestoides (Palmqvist, 1952). A mature female positions herself at right angles to a stem surface and waits for a male to climb up the stem. The male mounts the female and copulates. The female then bores a hole into which she and the male disappear. After about eight days the male reappears and the female also leaves the gallery. There is no information on recognition.

5.52.16 LYCIDAE

Aspects of courtship and mating behaviour are described for Calopteron terminale (Burke, 1976) and Metriorrhynchus semiflabellatus (Poulton, 1913), but no information is presented on recognition.

5.52.17 DRILIDAE

Females of Drilus flavescens, and D. mauritanicus secrete pheromones on the low leaves of plants to attract males (Balduf, 1969).

5.52.18 PHENGODIDAE

Females flash to attract males (Balduf, 1969).

In Zarhipis integrepennis haemocoelic insemination occurs (Tiemann, 1967; Wojcik, 1969a&b). The males are attracted to the larvi-form females by scent, although they are also luminous.

5.52.19 LAMPYRIDAE

The Lampyridae have been relatively well studied owing to their luminescence, emitted in flashes and serving to attract the sexes prior to copulation. (Balduf, 1969, Buck & Buck, 1972; Lloyd, 1964, 1965, 1966, 1968, 1972, 1973a, 1973b).

This mechanism is reviewed by Lloyd (1973b)

1. Both sexes are attracted to the flash rhythm of the males of their species.

2. Males detect approaching females and modify their luminescent behaviour in ways that stimulate females to land near them.
3. Recognition cues, other than flash rhythm, are detected as flying males and females are near to swarm trees.
- 4a. Females land near and observe specific males.
- b. Males land and flash in synchrony with nearby males.
5. Other types of behaviour bring individual males and females closer together.
6. A change in communicative channel occurs in the terminal stage of courtship before a male and female make physical contact.

Inter-specific discontinuity in modulation pattern and frequency is common in the signals of all fireflies and is probably involved as a reproductive barrier.

At some point when a male and female are very close, communication may be accomplished by non-visual signals. Pyrophorus pellucens (Elateridae) and Pteroptyx spp. may switch to chemical signals, and some fireflies are known to use pheromones.

Lloyd (1973a) suggests that the degree of development of behavioural mechanisms for avoiding hybridisation is a function of the incidence of related sympatric species with which hybridisation might occur. Significant elements in flashes for reproductive isolation in Melanesian fireflies (Lloyd, 1973a) are:

1. the duration of male flashes.
2. the period of flashes or flickered phrases in long series.
3. the period of flash or flicker modulations within phrases.

In addition, when the male is mounted on the female, in Pyractomena dispersa he repeatedly taps the abdominal tergites of, apparently unresponsive, females with his lateral lobes while the aedeagus is extruded but remains external. After tapping several

times the male extends the tip of his abdomen posteriorly to make probing movements with the aedeagus. This process is repeated until intromission is achieved.

The actual copulation process is similar in all species.

5.52.20 CANTHARIDAE

There is no information on mating behaviour in the Literature on the Cantharidae. Original observations are included here.

Cantharis nigricans

Males and females were observed in cages on damp filter paper, and on umbelliferous flower heads in large breeding cages. When first placed together both male and female beetles remained motionless for a few minutes. Then a male approached a female by running towards her, and climbing onto her dorsum using his mandibles for gripping. During this time the antennae were waved up and down, then finally the female abdomen was clasped with all three pairs of legs. Often during the approach phase the female made contact with the male first, by beating her antennae over his elytra. If the male turned around at this stage the female ran a short distance away and returned to the same spot whereupon the male moved around to mount the female.

During mounting the male fore legs clasped the female just behind the base of the elytra, the mid legs around the middle of the elytra and the hind legs around the apex of the elytra. All three pairs of legs were held right around the abdomen to the ventral side. The male head remained level with the base of the elytra with the maxillary palps touching the female.

The female continued walking, as the male mounted, and finally became still while the male extruded and inserted the genitalia into her genital orifice. Prior to insertion the male sometimes rubbed

the aedeagus around the area of the genital opening. Often during insertion the mid legs of the male were seen to hold the hind legs of the female to restrain her tendency to kick him and so prevent him from mounting.

After insertion of the genitalia the female either walked around, which caused the male to fall off backwards, and dragged the male behind her on the ground, or, freed her legs from the grip of the male and kicked him, during which time the male was pushed backwards. The male remained in this position with his head and pronotum raised at right angles to the abdomen and rested on the reflexed hind tarsi. During intromission the antennae and palps were vibrated and there were dorso-ventral contractions and telescopic movements of the abdomen. The male sometimes attempted to climb back onto the female but did not grip her in any way and so was forced backwards due to the kicking of the female. The female occasionally turned around to nip the male elytra with her mandibles.

Intromission in three pairs lasted 45, 50 and 65 minutes. Just prior to the end of intromission both the male and female became suddenly very active.

General Observations

Males have been observed to approach a mating pair, climb onto the female and assume the initial mating position, with the fore, mid and hind legs clasped around the abdomen. The genitalia were also extruded and intromission was attempted. Obviously this never succeeded and the male walked away. During this attempt the mating pair were not disturbed.

It is interesting that on several occasions a second male was attracted, in this way, to a copulating pair and not to other free females. Perhaps this, coupled with the male tendency to run at and after females prior to mounting, indicates that the female

produces some kind of chemical attractant.

Cantharis cryptica

Mating behaviour is very similar to that of *C. nigricans*. Males rapidly approached the females and grasped them around their elytra with the mandibles while mounting. The females' reaction to this was often aggressive, and frequently the pair struggled before separating. Male to male behaviour was also aggressive.

In the normal approach prior to mounting, the male rapidly advanced towards the female from behind, placed his mandibles at the apex of the pronotum, or base of the elytra, and gripped her hind legs with his. Sometimes the female only remained still long enough for the male to extrude the genitalia, then upon freeing her legs from the grip of the male, walked away dislodging the male. The male often attempted to remain attached to the female, as she ran, by clasping her hind femora with his mandibles. During this behaviour, the female often turned to face the male, whereupon a struggle, with the legs entwined, followed and the male attempted to regain his mounted position.

During copulation the pair remained in the mounted position. In this position, the male held his antennae down and slightly posteriorly, with the mouth parts resting on the apex of the pronotum. The male subsequently moved to a more posterior position with the head resting just behind the base of the elytra. The female antennae were held upwards during this time. The male fore legs gripped the female abdomen posterior to the mid legs; the male mid legs gripped the abdomen behind the female's hind legs; and the male's hind tarsi rested on the apex of the female elytra and around the abdomen. Throughout copulation the pair "leaned" to one side, the male occasionally vibrating his antennae down and forwards over

the females mid legs.

Termination of copulation was not fully observed, but intromission lasted 58 minutes ($n = 1$). Following copulation the male genitalia remained extruded for a few minutes, the lobe on the dorsal side and the ventral parameral lobe moving together like pincers.

Cantharis nigra

Mounting followed the same pattern as in the other species of Cantharis. The male mounted after touching the female's exposed apical abdominal tergites with his antennae. While mounted the male antennae were held well back over his body, while the maxillary palps touched the female pronotum. The female antennae were held forward and horizontal.

Just prior to the termination of intromission, the female became very active and moved all three pairs of legs. At the same time the male began to move and the genitalia were withdrawn. Following disengagement, the male remained in the copulatory position for about 30 seconds before dismounting.

Rhagonycha fulva

Observations were made in a tall breeding cage, on umbelliferous flower heads. Contact between pairs consisted initially of antennal fencing or antennation and palpation of the hind abdomen. Unreceptive females curled their abdomens ventrally. During mating the female often continued to feed on pollen. Once a pair were in copula, other males converged onto the same flower head and often climbed onto and over the mating pair. Several males came independently and attempted to mate with the engaged female by extruding their genitalia between that of the mating male and female. Sometimes a male remained mounted on an unreceptive female and occasionally rubbed

her abdominal tergites with the dorsal plate of the genitalia.

Other males were not attracted to pairs, where the female kept her abdomen ventrally curled to prevent mating.

One pair were observed mating for 24 hours. During this time both the male and female vigorously beat their antennae; the male beat his over the head and elytra of the female. The female seemed to beat her antennae in response to those of the male, but antennal contact with the male was not made.

Rhagonycha limbata

The male approached the female and either made initial contact with the antennae, or immediately mounted the female without any precopulatory behaviour. Upon mounting, the male genitalia were immediately extruded and inserted into the female. A receptive female remained completely still, whereas an unreceptive female curled her abdomen ventrally and dislodged any males which attempted to mount.

During copulation the hind legs of the male remained behind on the substrate and the fore and mid legs gripped the sides of the female elytra. The male constantly waved his antennae up and down on each side of the female head. Throughout this antennal movement the female was not touched except on occasions when such action may have acted to passify her. If the pair were disturbed during copulation the female waved her antennae and the male vibrated his vigorously, touching the female's head and eyes. The male also sometimes rubbed the female scutellum with his maxillary palps.

The female terminated copulation by curling her abdomen beneath her and walked away. Thereby, she dislodged the male and dragged him behind her until the genitalia were withdrawn.

The duration of copulation was observed to be about $3\frac{1}{2}$ minutes.

General Observations

Interspecific behaviour between three sympatric species was observed.

♂ R. lignosa x ♀ R. limbata

♂ R. lignosa x ♀ R. testacea

In both cases there was no reaction from either of the pair.

Malthinus flaveolus

The male mounted the female dorsum from a posterior position, and when coupling was achieved the male rotated 180° into an end to end position. This is in contrast to the mating position in Cantharis and Rhagonycha. Initially when the male was in the mounted position, his abdomen pulsated rhythmically and the mid and hind legs were moved along the female's body. The mid legs clasped around the female abdomen and met on the ventral side. The hind legs touched the apex of the female elytra. Throughout copulation the female generally remained still, whereas the male occasionally moved individual legs up and down on the spot. If the female walked around, the male walked backwards behind her. At first during copulation the male and female antennae were held horizontal and posteriorly, then subsequently their antennae projected anteriorly and slightly upwards.

As in Cantharis and Rhagonycha there is a dorsal plate on the male genitalia. This remained external to the female sternites during intromission, while the rest of the aedeagus was inserted into the female.

If the pair were disturbed during mating, as they often were by other males attempting to mate with the engaged female, the male turned back into the original mating position only later

resuming the end to end position.

The duration of copulation in two pairs was $6\frac{1}{2}$ and $1\frac{1}{2}$ hours respectively.

5.52.21 DERODONTIDAE

Mating behaviour of Laricobius erichsoni is described by Clark & Brown (1958). The male mounts the female on the side, sometimes with a second male attached to the opposite side. No details of recognition are given.

5.52.22 DERMESTIDAE

Owing to their status as stored product and household pests, 2 genera in particular have been studied in detail.

Beal (1954) in his studies on Trogoderma sternale, T. maderae, T. grassmani and T. simplex concluded that preceding copulation, their behaviour is practically identical. Males in closed petri dishes appear to be actively sexually stimulated only when their mouthparts or antennae come into contact with the setae on the dorsal surface of the female. Unmated males and females move at random, but after this type of contact the male immediately attempts to mate. After rotating and bringing his abdomen into contact with that of the female the male extrudes the genitalia and strokes the female pygidium with the phallobase until the ovipositor is extruded, when copulation can follow. This process may continue for many minutes with an unreceptive female.

It was shown that in T. sternale, T. maderae, T. grassmani, T. simplex and T. variabilis the females only respond to sexual stimuli from males of the same species. However, the males of T. sternale, T. maderae, T. grassmani and sometimes T. variabilis were stimulated to become sexually active after coming into contact with the dorsum of any of the species.

T. inclusum is similar in that males do not perceive females even when only a short distance away (Wodsedalek, 1912). A male, on coming into contact with a receptive female, rubs his antennae

against her abdomen; then after rotating into the mating position copulation follows.

A female sex pheromone is produced in T. granarium and T. glabrum. T. granarium has been studied by Hadaway, (1956); Finger et al, (1965); Levinson et al, (1970); Karnarvar, (1972); Chaudhary & Kapil, (1976); and Hammack & Burkholder, (1976). Mating follows shortly after emergence, and males congregate around a female pupa since the sex attractant is secreted at this time. On coming upon a female, the male palpates her elytra and abdomen. This acts as a stimulus for the female to raise her abdomen and extrude the ovipositor so that intromission can occur. The pheromone acts as an aggregation scent and, after contact, as an aphrodisiac.

A female sex pheromone has been reported in T. glabrum. However, Wojcik (1969a) observed that male sexual activity was only stimulated after contact with the dorsum of the female.

After the initial contact with the female, the male moves to palpate and antennate the female abdominal apex. Then whilst extruding the aedeagus the male rotates so that the abdominal apices are brought together and the aedeagus rubs the apex of the female abdomen. The lateral lobes sometimes tap the females last sternite prior to intromission.

Vick (1973) reports inter-specific matings between T. glabrum and T. inclusum. The males transferred spermatophores in both reciprocal crosses but sperm did not usually reach the spermotheca. Where females were given a choice of males, 24% of T. inclusum females mated with T. glabrum males, and 20% of T. glabrum females mated with T. inclusum males.

Mating in Anthrenus flavipes is described by Wojcik (1969a&b). The male approaches the female from any direction but does not appear to perceive the female from distances over 2 cm. Often the male

first palpates the female elytra before mounting. At times during copulation the male mid legs may rub along the forward lateral edges of the female elytra, but this does not appear to be related to her restlessness.

5.52.23 BOSTRICHIDAE

Mating behaviour has been observed in 3 genera.

Aziz and Sitarman (1948) describe mating in Dinoderus ocellaris, Wright (1960) in Lyctus planicollis and Tilden (1953) in Psoa maculata but no information is given regarding recognition and courtship.

5.52.24 ANOBIIDAE

Mating behaviour has been observed in 3 genera. Sharp (1916) dissected pairs of copulating Ernobius consimilis and E. mollis. During copulation the sexes stand end to end. The apical abdominal segment of the female enters entirely into that of the male so that the hooks and processes of the male aedeagus are brought into contact with the entrance of the vulva. The median lobe of the male enters the vulva and the lateral lobes remain external lying one each side of the vulva.

Externally sympatric Ernobius species are very similar, however, the male aedeagus shows very striking differences with an elaborate development of asymmetrical lobes. Such differences in the aedeagus are also seen in Xestobium, Anobium, and Dorcatoma (Freude, Harde & Lohse, 1969).

Coffelt (1971) and Tobin and Smith (1971) indicate that a sex pheromone is produced by female Lasioderma serricorne. The pheromone, which is produced at the apex of the spiculum ventrale, causes the males to elevate their antennae and extend their prothoracic legs over an attractive range of 40 cm. Two out of ten antennectomised males were successful at copulation although location of the female

was delayed longer than the usual 20-60 seconds. Upon reaching the female, the male examines her, mounts from behind and intromission follows very rapidly. Females are attractive to males prior to their first mating and after each oviposition, but not during the intervening time.

Acciavatti (1972), in discussing the ecology of Ptilinus ruficornis, mentions that adult courtship involves a female sex pheromone.

5.52.25 PTINIDAE

Woodroffe (1958) remarks that mating is rarely observed in ptinids.

Ptinus clavipes is a polymorphic species with three female forms. There is a pronounced mating reaction associated with definite postural behaviour in one female form which is known as the "calling posture". In this the female bends the fore legs and straightens the hind legs until she is virtually standing on her head. During this time the ovipositor is slowly extruded and withdrawn. This pose attracted other females who appeared to imbibe fluid from the tip of the abdomen.

There are striking differences in the genitalia between some species of Ptinus (Freude, Harde & Löhse, 1969).

5.52.26 CLERIDAE

Mating behaviour has been observed in 2 genera.

The Cleridae mate on flowers and on trees attacked by bark beetles and other wood inhabiting Coleoptera (Balduf, 1969). Berryman (1966) only mentions that in laboratory conditions mating occurred whenever the male and female come into contact in Enoclerus lecontei. Hitchcock (1963) discusses a possible means of sex recognition in Necrobia rufipes. Using an olfactometer, it was concluded that odour played little or no part in sex recognition since a male was unaware of a

female until chance contact was made. The male antennae are used for orientation and mating still occurred if the antennae were removed. Upon mounting the male appears to nibble at the base of the female elytra with the mandibles and maxillae. Males were seen attempting to mate with a wooden dummy in which elytra of a female were attached to the model. The female may be distinguished from males by the presence of forwardly projecting setae on the female elytra. These have been considered to assist the male in maintaining his position during copulation, but it is possible that these may afford a means of recognition. Evidence from experimental trials using models indicates that these, or other attributes of the female elytra, are important in sex recognition. Necrobia species develop and live in the same habitat so there is no need for elaborate mechanisms for bringing males and females together, simple contact stimulus is sufficient.

5.52.27 MELYRIDAE

Mating behaviour has been observed in 5 genera but only in the Malachiinae.

The males of many malachiid species have secretory excitator organs on different parts of the body (Matthes, 1962a; 1962b).

Male Axinotarsus marginalis have an elytral and cranial organ in which there is a secretory apparatus which is offered to the female during courtship. The female manipulates the organ with her mouth parts during which the male may move his hind legs up and down.

Females of Anthocomus fasciatus are stimulated mechanically with the male saw-like antennae as well as with the elytral excitator organs (Matthes, 1971).

The males of individual malachiid genera, including Axinotarsus and Attalus, have modified 2nd tarsal segments on the fore legs which

are pectinate and used to anchor onto the female during copulation.

In malachiids population density and levels of activity determine the chance of sexual encounters. Recognition is normally visual (e.g. males of Troglops albicans) but contact-chemoreception and close range olfactory perception of the secretions helps to determine the sex of the partner.

The excitator organs are employed during the course of copulation.

The males of species with elytral organs first make antennal contact with the female and then rotate through 180° to present the elytral organs. The female bites the organ and tastes the secretion emitted from the excitator. Frontal stimulation, organ offering and the associated biting act are carried out repeatedly during courtship thereby increasing the "excitation" of the pair.

In Malachius marginellus face to face encounters between males and females result in hostile behaviour, consequently antennal contact is entirely bypassed in courtship. The male presents his elytral organ then the female rotates into an end to end position whereupon the male elongates his hind abdomen and touches the female hind abdomen.

Troglops albicans and Malachius bipustulatus have excitator organs in pits, on the fronto-clypeus of the head capsule, which are presented to the female during courtship. The male then moves to examine the female abdomen tip.

In M. bipustulatus recognition is by close range olfactory stimulation whilst, in M. viridis it is visual.

When a female is not immediately receptive the male alternates his presentation of the head-pit with tickling of the abdominal apex, until the female indicates her receptivity by remaining still.

The chemical nature of the excitation secretion is still unknown.

McAtee (1916) and Nielson & Henderson (1959) discuss mating behaviour in Collops vittatus. Prior to copulation the male persistently follows the female, frequently touching her abdomen with his antennae. During courtship the female mandibles are widely spread so that their tips rest in the depressions in the modified anterior surface of the enlarged antennal joints of the male. The male antennae are held horizontal and parallel. If a pair separated they would return to this position.

5.52.28 CUCUJIDAE

Two genera have been studied by Wojcik (1969a&b) and both are pests of stored products.

In Cryptolestes pusillus the male does not seem to perceive the female until his antennae touch her. On frontal approach both beetles' antennae touch, alternatively on approach from behind the male touches the tips of the female elytra and abdomen with his maxillary palpi. From both situations the male moves to the side of the female and places his antennae horizontally along the side of her body, pushing her body with his mouthparts. The male then moves to the apex of the female abdomen which he palpates. The male then places his antennae horizontally forward, one along each side of her body, whilst intermittantly rising on his legs and spasmodically twitching his body. The genitalia are then extruded and the male turns through 180° and backs onto the female, pushing hard, until copulation is achieved. Throughout intromission the female remains still.

The pair also exhibit post copulatory behaviour. After withdrawal of the genitalia the male walks in front of the females head and crosses her antennae dorsally with his. He then moves forward and touches her head, particularly the mandibles, the clypeal area, eyes and surrounding area with his mandibles and maxillary palpi.

The female repeats these actions, and the activity may continue for 1 - 2 minutes.

Differences between C. pusillus and C. ferrugineus occur in the precopulatory behaviour. C. ferrugineus does not move to the side of the female but remains at her rear, and postcopulatory behaviour is absent.

Similarly males of Oryzaephilus mercator do not perceive females until antennal or palpal contact is made. The male then moves directly to the rear of the female, touches the tip of the abdomen with his maxillary palps and mounts the female. During copulation the female antennae are held at 90° to the body axis, and those of the male held forward and horizontal sometimes touching the females. The male mandibles nibble the central ridge of the female prothorax, while the maxillary palps touch the prothorax. If the female is restless nibbling and palpating become more vigorous.

5.52.29 CRYPTOPHAGIDAE

Mating behaviour in 2 genera is discussed. In Atomaria ruficornis, Evans (1961) describes the function of the genitalia during copulation.

Hinton & Stephens (1941) report that during copulation in Cryptophagus acutangulus the male moves his antennae rapidly up and down along the sides of the female pronotum, accompanied by lateral twitching of the head and pronotum and sometimes of the mid and fore legs.

5.52.30 COCCINELLIDAE

Mating behaviour has been observed in several genera but no information is published on courtship and recognition (Balduf, 1969). Puttaswamy & Channa Basavanna (1977) record the duration of copulation for Stethorus pauperculus and similar limited information is given for Coccinella septempunctata by Wang et al (1977).

Hodek (1967) discusses aggregation and hibernation in predacious coccinellids and suggests that the bringing together of the two sexes from different sites has the adaptive value of raising the probability that sexes of rare species meet and interbreeding is prevented. Diapausing coccinellids mate partly prior to diapause but mainly at the end of hibernation before the aggregations disperse.

In Epilachna indica (Pradhan, 1935) the male, after seeking the female, briefly touches her with his antennae and then immediately mounts from any direction. The male extrudes the genitalia and probes the female genital opening. On obtaining the correct orientation the male deflexes the lateral lobes and places them beneath the last two sternites of the female. The end of the lateral lobes gain leverage against the articulation between the second and third sternites from behind. The male siphonal sheath is applied against the ventral pair of plates of the female genitalia; the lateral lobes and the siphonal sheath acting together as a steadying apparatus.

Mating behaviour of Coccinella septempunctata is described.

Coccinella septempunctata

Courtship was not observed. Initially in copula the male was mounted on the dorsum of the female with his fore and mid legs gripping the sides of the female elytra. This enabled the male to push the aedeagus into the female genital orifice. Once the aedeagus was inserted the male performed side to side rocking movements over the female. At first the side to side movements were slow and regular, and these were followed periodically by the male moving slightly forward over the female and repositioning his fore and mid legs anteriorly. The hind legs were held backwards well clear of the female and in mid air. For about 15 minutes the slow rocking movements were interspersed with periods of rest when the male thrust the aedeagus back and forth every 2 - 3 seconds. There were short

periods when the male stroked the female hind abdomen or the edge of the elytra with his hind femora. The hind tibiae were also used for this purpose. For the following 20 minutes the side rocking became more violent, although pauses between bursts of rocking became longer. During the side rocking the palps, and setae beside the male genitalia, rubbed alternately over the two sides of female sternite VIII. In the longer periods between side rocking the male more frequently stroked the female abdomen with his hind legs.

Towards the end of copulation the side rocking resumed and developed into short, side to side shakes interspersed with leg stroking.

The duration of copulation was 90 minutes.

5.52.31 RHIPHOPHORIDAE

Besuchet (1956), discussing mating behaviour in Rhipidius spp., notes that the females secrete a sex pheromone which is perceived by the long fan-like antennae of the male. When a male locates a female he immediately climbs onto her dorsum, then moves posteriorly to seize the female ovipositor with the aedeagus. The ovipositor is pulled until it is completely evaginated. Meanwhile the male abdomen is agitated and he drums on the back of the female with all six legs and spreads out his antennae.

A fertilised female does not continue to produce the sex pheromone.

Similarly, in Rhipiphorus smithi, a female sex pheromone attracts males over considerable distances mediated by their complex antennae (Linsley et al, 1952). Mating generally follows immediately upon emergence of the female and several males may be in attendance. A male approaches a female and attempts copulation without preliminary courtship. Sexual contact is first made from a dorsal position, the male then moves laterally from where copulation is completed. At

intervals the male strokes the thorax of the female with his fore legs and mouth parts. Termination of copulation is initiated by the male.

5.52.32 TENEBRIONIDAE

Mating behaviour has been studied in 7 genera, some in considerable detail owing to their status as pests of stored products.

In Pimelia sardia males recognise females by their specific odour, using their antennae. The male antennae are wiped back and forth on the fused female elytra, then the male attempts to mount the female. A receptive female remains still often burying her head in the substrate, (Dzimirski, 1963).

Bolitotherus cornutus is a nocturnal species living in fungi. Prior to mating the male clasps the female so that the ventral surface of his abdomen rests on the dorsal surface of the female thorax. When in this position the male rubs the ventral surface of his abdomen across two prominent tubercles which project from the female's thorax. This produces a distinct rasping sound, audible at a distance of about 6 - 8 feet. This is continued for one or two minute periods interspersed by one-two minutes of quiet. At the end of the periods of rasping the male reverses his position and copulates with the female. The rasping may be carried out at different periods for several days before and after copulation and during the egg laying period, usually at night (Liles, 1956).

In Blaps pinguis and B. requieni the males mount the female briskly, apparently without olfactory or other examination, and males have often been seen descending from the females a few minutes later after a futile mating attempt. Altevoigt (1958) regards this as the male mounting the wrong species. In Blaps mortisaga the males are thought to produce a sexual odour from an organ on the hind abdomen which lures females. The precise functional biology of this remains

unknown. Males remain in the dorsal riding position after copulation is complete, and throughout egg laying.

Males of Eleodes hispilabris and E. connexa have a short pointed pre-apical spur on the prothoracic femur which hooks into a protruberance on the female elytra during mating (Haverfield, 1965). The male approaches the female waving his antennae and antennates the genital area of the female. The male mounts the female whilst tapping the elytra, thorax and head with his maxillary palps and anteriorly projected antennae. The male "massages" the female mesothorax with his prothoracic tarsi and strokes her antennae with his. At this point copulation may occur. If the female is not receptive at this time her genital plates remain closed, although the male may remain mounted for several hours.

Some matings have been observed without prior courtship. This occurs in males which have been caged separately for several months. Males have also been seen to mount other males particularly those already in copula and frequently these mountings occurred back to front. Haverfield suggests this may be because a female sex attractant might be produced which has contaminated the copulating male's head and appendages.

Stanley & Grundmann(1965) and Wojcik(1969a&b)describe mating in Tribolium confusum. The male does not appear to perceive the female from distances over 2mm. Mounting occurs on making contact with the female, with or sometimes without accompanying antennation. Frequently the male touches the hind margins of the elytra with his maxillary palps prior to mounting. During copulation the female prothorax may be antennated, palpated and touched with the male mandibles. The ventral surface of the fore tarsi may be rubbed along the sides of the female elytra. Intromission is only achieved if the female relaxes the sternite VII, and when this does not occur readily the

male repeatedly extends and withdraws the aedeagus and taps the female abdominal apex.

The males are not discriminating in their selection of mates and may try to copulate with males of their own species, T. castaneum or even dead beetles.

Doyen (1966), August (1971) and Gerber (1973) discuss mating in Tenebrio molitor. The male has a large process on the inner protibial angle which is accompanied by an increase in the extent and density of the setal fringe along the posterior protibial margin, and an increase in size of the tibial spines. This is used to hook under the epipleural margins of the female elytra during copulation.

Sex pheromones are released by both sexes. The sex pheromone produced in the female rises to a maximum within a week after emergence as does the male response to it. The male pheromone serves to aggregate the females. On perceiving a female, the male waves his antennae and this is alternated with periods of quiescence. The male takes a few steps, stopping periodically to raise and vibrate his antennae and palps and to extend the prothoracic legs, which raise the anterior part of the body. This activity becomes more continuous until the male contacts the female when he immediately attempts to copulate. Mounting involves female elytral, pronotal and abdominal stroking with the antennae, accompanied by rapid strokes of the prothoracic legs against the sides of her elytra.

Wojcik's (1969a&b) report of mating in Tenebrio obscurus indicates that behaviour and mating position are similar to T. molitor, although sex pheromones are not involved and a male does not perceive a female from more than 5 - 10 mm.

In two species of Androchirus which are allopatric there is no elaborate courtship, and behaviour during mating is relatively simple (Campbell, 1966). In the male the anterior tarsi are broadly

expanded and curved to grasp the female during mating. The males also have greatly enlarged and spoon shaped lobes on the sternite VIII which are used during coupling to hold the female abdomen and help guide the genitalia to the female gonopore. Both species have almost identical behaviour, the main difference being in the position of the female legs (horizontal in A. erythropus, vertical in A. femoralis), and in the use of the male fore legs.

Mating is carried out in two phases: 1) dorsal phase, which includes initial contact as far as genital coupling, and 2) posterior phase, where the male stands behind the female, and pulls her ovipositor.

Inter-specific matings were attempted with the two species, and reciprocal crosses were successful. At most inter-specific mating trials the female attempted to avoid the male, but the major factor in the successes was the ability of the male to catch and hold the female in spite of rejection. Eggs and first instar larvae were obtained from 2 crosses.

5. 52. 33 MELOIDAE

Mating behaviour is available for 18 genera.

In the Meloinae, courtship is elaborate, mating periods are long and there is a secure genital coupling mechanism. Females mate once before oviposition. However, in the Nemognathinae courtship is simple, the duration of copulation is short and there is no genital coupling mechanism. Females mate several times before oviposition.

In the Meloini, the courtship of Meloe (Meloe) strigulosus consists of tactile stimulation including dorsal manipulation of the female antennae of two distinct types; antennal tapping, which is unique, and antennal grasping, which is common to the subgenus. Similar behaviour is found in M. impressus and M. dianella. In M. angusticollis and M. campanicollis the copulation attempt as a

ritualised component of male display is absent. The phases of copulation in Meloe according to Pinto (1972a) are as follows.

1. Preliminary phase: including approach and mounting.
2. Dorsal phase: dorsal riding, antennation and leg rubbing.
3. Genital phase: posterior riding and genital insertion.

Most of the behaviour has been observed in species belonging to the tribe Lyttini.

Pyrota species are strictly phytophagous and most species are specific to one family and to one genus. As sexual behaviour occurs on the food plants this may act as a reproductive barrier. Blister beetles are non-aggressive and the male approaches and mounts, or otherwise establishes contact with the female as soon as he discovers her, without preliminary signalling or testing of response. Courtship involves physical stimuli and continues for a long time. Sexually motivated males search for females and approach directly when one is found. If the female remains still, courtship begins and involves a sequence of activities performed repeatedly and continuously by the male. The different categories include: dorsal antennation, palpation and rocking in the dorsal position, moving backwards and forwards, then leg grasp, insertion of the maxillary palps between the female elytra, lifting the posterior abdomen of the female and abdominal antennation in the posterior riding position. Inter-specific differences involve the manner in which the act is performed, its frequency of occurrence and its precise temporal relationship with other acts. During copulation the lateral lobes of the male genitalia function as guides for the aedeagus by pressing on each side of the female gonopore. Dorsal and ventral hooks on the aedeagus catch onto the vagina walls to provide a firm coupling mechanism. Despite this, Selander (1964) infers that all species of Pyrota ought to be

compatible.

Ethological divergence is evident for species which occur in sympatry with related species. This is also prevalent in Meloe and Epicauta, but is most striking in Pyrota.

Phodaga alticeps shares the basic pattern of meloine behaviour with certain unique features (Pinto, 1972b). Male stimulation of the female is tactile, curling his antennae around those of the female and stimulating her with the maxillary palps and mid legs. Such a display alternates with quiescence. In Negalius the male fore legs are modified for clasping the female pronotum, and the mid legs for stimulating the female maxillary palps. Cordylospasta of the same subtribe does not have these modifications (Pinto, 1972b).

Courtship in three allopatric species of Tegrodera is distinct from all other meloids (Pinto, 1975). The male display includes antennation, performed while facing the front of the female's head. This involves grasping the female antennae with his own and repeatedly pulling them in and out of two corresponding grooved depressions on his head. The following inter-specific matings have been observed,

Male T. aloga x female T. erosa

Male T. latecincta x female T. erosa

Males of T. erosa will court female T. latecincta.

In Cysteodemus, mating behaviour represents a condition between that found in the Meloinae and Nemognathinae, although there is no qualitative difference between the two species studied (Pinto, 1977).

Megetra species follow the typical meloine pattern of mating behaviour. Once mounted the male strokes the corresponding antennae of the female with alternate antennae. The stroke begins at the base of the female antennae and continues to the apex. The male stroking surface of the antennae lacks dense pubescence and is sparsely set

with tiny erect setae.

Males of Lytta nuttali are very active in courtship, and when mounted repeat a cycle of three stereotyped stimulatory activities. The male uses both antennae to stroke alternately the tips of the female antennae which he holds upright with his forelegs. The male brushes the ends of the female elytra and tergite VIII with the long bristles on his eighth sternite with rapid lateral vibrations of his abdomen. The male also repeatedly probes the end of the female abdomen with his aedeagus whilst attempting to establish genital contact. This cycle of courtship lasts from a few minutes up to one hour. Females appear to be attractive to males around the time of oviposition and it is suggested that females produce sex pheromones (Gerber & Church, 1973).

Gupta (1966) reports a locking action by one ventral and two dorsal aedeagal spines in the accessory copulation apparatus of the female in Lytta vulnerata.

Matthes (1972) regards face to face antennal contact as a means of sex recognition in Lytta vesicatoria, either mediated by a mechanical receptor or chemoreceptor process. In this species antennal stimulation occurs in the mounted position. The female's antennae lie in a bow shaped recess of the male's first tarsal segment which can be closed using a tibial spine. The male then begins to vigorously "stimulate" his partner. Lytta variabilis males hold the female antennae with their antennae and press them alternately into a short-haired pit on each side of his head. This may be tactile stimulation from the hairs, or contact chemoreception from a secretion in the pit. Similar structures have been detected in 22 Lytta species, but not L. vesicatoria (Selander, 1960).

Species recognition in Cerocoma ["]schafferi is visual at a limited distance (Matthes, 1970). A male flying near another individual of the same species immediately lands on that individual's dorsum and begins to copulate. This type of approach does not enable the male to perceive the sex of the other individual; however, the reaction of the individual determines whether the right choice was made.

Upon meeting a female the male begins courtship and mounts immediately. The male raises his fore legs and beats them in an extremely vigorous fanning movement. At the same time the abdomen moves rhythmically over the female thereby increasing the stimulation of both partners. Frequently one of the hairy fore legs is pulled through a cavity in the maxillary palps in which a secretion is emitted. The secretion is then scraped onto the antennae and the fanning movement of both legs and antennae provide olfactory stimulation of the partner. It is not known whether such a secretion is species specific.

Pleuropompha species, of the subtribe Epicaulina, do not have a tactile display or dorsal mounting. These are replaced by an antennal display which is non-tactile. The timing of antennal fanning may be a significant inter-specific difference. The male antennae have specific structures or pores which may have a glandular chemical function, the fanning assisting in evaporation and dispersal of the chemical to the female (Pinto, 1973).

Linsleya spp. are very near to Epicauta and Pleuropompha. Recognition is visual and olfactory and courtship is performed with the male positioned behind the female and lacks any tactile aspect, (Selander & Pinto, 1967; and Pinto, 1973).

Rayah (1973) observed that some tactile display occurs in Epicauta aethiops and the male may rub the posterior end of the female abdomen with his antennae.

In contrast, in the Nemognathinae there is a simple courtship in which the male strokes the female with his antennae and palps after which mounting and copulation occurs (Balduf, 1969).

5.52.34 CERAMBYCIDAE

Pairing in cerambycids occurs either immediately after emerging from the pupa or in some species after a maturation feed.

Pairing takes place mostly in the area of the breeding place or in flowers. The meeting of the two sexes is difficult since they do not emerge at the same time; the females emerge later than males. Females of some species are sought by males using olfactory organs on the antennal segments (Butovitsch, 1939).

Duffy (1946) discusses mating in Prionus coriarius but does not give an indication how sex recognition is achieved. However, the male "springs" onto a prospective mate often at the same time having to ward off persistent rivals. During copulation both beetles stridulate loudly and the male palps continually rub the female thorax.

In the Lepturinae the olfactory sense may be well developed but is not generally used for mating. Most Lepturinae and Cerambycinae congregate in sunshine on flowers of Compositae and Umbeliferae for feeding and mating. The male recognises the female only at very short distances after touching with the antennae. Males are not stimulated to mate when their antennae are removed, therefore there may be a sex specific odour, particularly since males may mount other males which have been in copula (Michelsen, 1963).

Females are generally not readily receptive and may attack a male at this time biting off his antennae or legs. The male mounts "by surprise" and begins to stimulate the female with combined

licking (where the palps are stroked on the dorsum of the female) and tapping (where the head is rhythmically depressed so that the mouth parts are tapped on the female e.g. Aromia moschata (Duffy, 1949). The male may also scrape and bite the pronotum or antennae, make abdominal movements, pull the ovipositor and wipe and strike the female abdomen.

In Strangalia species the male mounts the female until his head is level with hers, then pulls the head upwards by grabbing her antennae with his mouth parts. The male then probes the female abdomen with the aedeagus to contact and fasten to her ovipositor. In copula the male releases the antennae and periodically licks and taps between the bases of the antennae.

When disturbed a pair may stridulate, but this is not used as a courtship song as is supposed in Clytus arietus (Cerambycinae). However, several lepturines and cerambycines stridulate during sexual activity. Male stridulation may be coupled to stimulatory activity and the sound is different from that produced when a pair are disturbed, e.g. males of Leptura sexguttata and L. rubra, and both sexes of Clytus mysticus and Plagianotus floralis, (Michelsen, 1966; and Chemsak, 1966). Rhagium mordax males recognise females by sight at longer distances and also select partners according to size. Asemm striatum, Tetropium castaneum and Clytus mysticus males seem to be stimulated by the female, who upon meeting the male, turns and runs away. It is not known whether the variations in stimulatory behaviour together with restless behaviour in the female serve as part of a reproductive barrier. Inter-specific mating is rare but has been observed.

Michelsen (1963 & 1966) compares stimulatory behaviour in 23 genera. In the Cerambycinae the first stimulus to mating is thought to be visual and the second is a sex specific odour which

occurs in a low concentration relative to the sensitivity of the chemoreceptors.

Neocompsa textilis var. alacris males are stimulated when physical contact with a female is made, after which the male pursues the female. In this species, Tragidion armatum and Xylotrechus nauticus, the male upon mounting, immediately initiates licking behaviour on the female scutellum or the front margins of the pronotum with the maxillary palps. This serves to quieten the female and stimulates her to extend the ovipositor (Chemsak, 1963, 1966). There is no palpation of the scutellum or elytra in Oeme costata (Chemsak, 1965)

In Penichroa fasciata coupling may be preceded by a struggle between males, where the winner couples with the female, who plays no part during the struggle (Puppin, 1973).

Funke (1957) discusses mating in several laminae. The time span between emergence and the first pairing is very different. The sexes find each other mainly in a specific place and at a specific time of day. An increase in flight activity, at least in males, increases the chances of the sexes meeting.

In Saperda populnea vision does not play a role in the detection of females, the males swarm and alight near females by accident. The sense of smell for sex recognition is only well developed in Mallosia spp. Contact is not necessary in Hylotrupes bajalus, Xylotrechus rusticus and Hesperophanes griseus and the females are all ardently pursued by the males. Active male antennal beating during copulation occurs in Saperda populnea, Tetrops praeusta, Phytoecia nigricornis and Pogonochaerus hispidus. In males of Oberea erythrocephala rhythmical and nodding movements of the head and pronotum are performed. In Saperda candida and Xylotrechus rusticus the females make rotating movements with the

outstretched ovipositor which, combined with olfactory stimuli, may attract males (Garland & Worden, 1969).

In Dectes sayi there is no ritualistic courtship but the male presses his mandibles or maxillary palps against the female scutellum during copulation (Piper, 1978).

5.52.35 BRUCHIDAE

Information on mating behaviour is available for 4 genera.

Males of Callosobruchus analis are not chemically attracted to the females but have a strong desire to mate and may mount other males temporarily. As soon as a male emerges from grain it searches for a mate. On approaching a female the male raises the fore and mid legs with which he holds the female abdomen. Sometimes before mounting the male touches the female pygidium with his antennae. If the female is unreceptive she kicks the abdomen of the male continuously with the hind legs. Termination of copulation is initiated by the female attempting to kick the male off by a few forceful backward strokes of the hind legs (Arora & Pajni, 1957).

In Bruchidius incarnatus newly emerging adults start mating as soon as they meet (El-Kifl & Metwally, 1971). The male is aggressive and insistent and strikes the female with his antennae. As in Callosobruchus analis the female initiates termination of copulation.

Johnson (1967) describes mating in Merobruchus and Stator but does not give information on courtship and recognition.

5.52.36 CHRYSOMELIDAE

Information is available for 11 genera, but only brief details are given and there is little regarding courtship and recognition.

Michelsen (1966) describes courtship in Donacia aquatica, where the male antennae often hit those of the female. During

mating the male performs a wiping action with his fore-tarsi on the female head and pronotum, which may touch the female antennae or eyes. Licking is observed during courtship and at the end of copulation, but this is weak and may be performed in the air just above the female dorsum.

In Liliocerus lillii behaviour is similar to the Lepturinae (Cerambycidae) where weak antennal movements are performed during courtship, at the beginning of copula and at the end of mating. Sometimes at the end of mating the male produces sounds while being kicked by the female.

Barrows (1979) discusses mating in Metriorhynchus bicolor and Cassida guttata where males mount the females, their antennae held forwards. Some pairs of C. guttata were seen in linear copulation.

In three courtships of M. bicolor, males approached resting females, mounted them and antennated the heads with both antennae simultaneously or alternately. A colour change occurs during copulation in adults of M. bicolor, from brownish orange with black spots to brilliant metallic gold. The function of this is thought to be 1. camouflage, 2. sexual receptivity, 3. mimicry.

Khatib (1934) reports that prior to copulation in Gallerucia birmanica, adults assemble together and by the touch of the antennae recognise their mates. An unreceptive female will raise her mid and hind legs. During copulation both males and females keep their antennae in constant motion but otherwise remain quiet. The female initiates the termination of copulation by kicking the male with her fore and hind legs so forcing him to loosen his grip.

Courtship in Aulacophora foveicollis initially involves the female facing the male in a straight line, she then catches hold of the male prothorax with her mandibles or fore legs (Mukerjee & Chandhuri, 1960).

Males and females of Agasicles spp. feed after emergence and when the female begins to look gravid the male displays sexual interest. The male mounts the female dorsum and advances anteriorly over her, to which the female responds by raising her abdomen. The female oscillates her body vigorously from side to side and the male positions his antennae between those of the female, and rubs them slowly against hers. The male then moves posteriorly for intromission (Maddox, 1968).

The male genitalia are often elaborately modified, particularly the apical parts, and differences between closely related species, which are otherwise morphologically similar, are striking (Freude, Harde & Lohse, 1966). Females also exhibit differences in the form of the chitinated spermatheca.

Following observations on galericid species, (S. L. Shute pers. comm.) the females are gregarious and when approached by a male, female receptivity is indicated by opening of the genital segment. Some antennal tapping and genital probing of the abdominal apex may occur; however, in general there is no elaborate courtship.

5.52.37 ATTELABIDAE

Only one species has been observed and there are no details regarding courtship and recognition (Jancke, 1934).

5.52.38 SCOLYTIDAE

Six genera have been studied. Most scolytids mate in galleries excavated in trees and all mate in the end to end position, with the female dorsum up and the male venter up. Sometimes both sexes are attracted by a pheromone. Virgin Dendroctonus females attract males and other females (and Ips). The effect of the scent is also to attract other members of the species to a suitable food source.

Doliopygus eximus males dig a burrow, from which the male

protrudes his elytral apex. The females then fly to the tree to search for males. Then follows an elaborate premating sequence (Jover, 1952).

1. The female pushes the male into the chamber.
2. The male pushes the female to the exterior and both leave the chamber.
3. The male scratches at the entrance and follows the female into the chamber.
4. The male grasps the apex of the female abdomen and pulls her to the exterior where mating is quickly completed.

Hylastes rugipennis have distinct premating stridulation (Oester, et al, 1978).

In the laboratory males are attracted to galleries of unpaired females and begin chirping when contact with the female is made. Upon male contact, most females responded by backing towards the gallery entrance and forcing the male to back out first. While backing out the male usually stridulates repeatedly, and brushes his antennae across the female elytra and strokes them with his fore and mid legs.

Five species of Dendroctonus have been observed, and courtship is basically the same in all cases, (Francke - Grosmann, 1950; Reid, 1958; Yu & Tsao, 1967; Rudinsky & Ryker, 1976 and Ryker & Rudinsky, 1976).

The female sits in a gallery and a male approaches by backward motion from behind and strikes the female elytra with the hind legs. Coupling then follows. Courtship of this type is similar in Ips chalcographus. Sex recognition is reported to be olfactory in Dendroctonus monticolae and is probably so in other species.

Dendroctonus pseudotsugae and D. ponderosae males stridulate

prior to mating. In males of D. pseudotsugae, attraction chirps are produced during burrowing through frass in the female gallery. After making contact with the female they are changed to interrupted chirps. Meanwhile the male jostles the female and strikes her with his forelegs and bites her elytra. At the same time the male scrapes his mandibles across the tubercles on the female elytra and produces loud grating noises. The female responds by orienting her heavily sclerotised elytral declivity towards the male and tilting so that the lower margin of her elytra protect her legs from the male mandibles. Both beetles then co-operate to produce a brood chamber. Several minutes before copulation a new courtship chirp is produced together with gentle nudging and biting of the female elytra. To mate, the male turns and gives simple chirps while backing up the gallery, bumping against the female and revolving into the venter to venter mating position. When the genitalia are engaged the male is silent.

In D. ponderosae the male emits interrupted chirps, both while fighting a rival male and when attracted to a virgin female's gallery. This behaviour was aggressive in both cases. When a chirping male touches a female she becomes silent permitting his entry into the gallery. However, a female chirps continuously, and will attack and eject surgically silenced males. This indicates a premating recognition function for the male's interrupted chirp. Non-aggressive courtship behaviour occurs in the gallery as the male stridulation changes to simple uninterrupted chirps just before mating. This includes stroking of the female elytra and abdominal apex with the male fore and hind legs. Females are silent during courtship.

In Eccoctogaster ventralis the female is stimulated to mate when the male presses his head on the female abdomen, and on turning when he places his posterior abdominal segments against those of

the female (Ashraf & Berryman, 1969).

E. multistriatus males court females at gallery entrances where this behaviour may be stimulated by tactile, sonic or chemical signals alone, or in combination (Bartels 1974).

Females of E. quadrispinosus rest in a gallery with the tip of the abdomen at the entrance. The male "titillates" the female venter with short upward strokes of the setal brush on his frons. This stimulates the female to receive the male and she responds with rapid, repeated outward thrusts against the male head which is held tightly pressed against her venter. After stimulation the male reverses and presses his venter against that of the female and copulation follows (Goeden & Norris, 1965).

In Ips pini, I. confusus and I. paraconfusus the male constructs the nuptial chamber and may struggle with, or turn out, unwanted females (Schmitz, 1972).

Wilkinson et al (1967) report that Ips spp. have stridulating organs on the head and pronotum. In I. calligraphus, pairs are formed when females are attracted to males in pine logs. Males may be accepted on the basis of their ability to stridulate (they produce long series of premating sounds). Virgin females stridulate prior to mating but not during copulation in I. calligraphus and I. confusus.

There is a vast literature on pheromone production and sex recognition in the Scolytidae which will not be reviewed here.

5.52.39 BRENTHIDAE

Only Brenthus anchorage has been observed. When in each others presence both males and females vibrate their antennae rapidly. The male moves about until he succeeds in placing his proboscis upon the female thorax or head, which then stimulates the female to

remain still. The male proceeds to rub the proboscis against the female head and thorax. As soon as the male mounts, the female begins boring into wood with her mouth parts. Courtship may continue after mating, until a second mating takes place (Malkin, 1949).

5.52.40 RHYNCOPHORIDAE

Information is available for 2 genera, but Hagley (1965) gives only brief details for Rhyncophorus palmarium.

Wojcik(1969a&b)gives details of copulation in Sitophilus granarius. The male approaches the female from any direction and does not appear to perceive her until contact is made, when he mounts immediately. Upon mounting the tip of the male rostrum touches, and may rub, the female prothorax to quieten her. At the same time the male antennae may tap the side of the female prothorax, although for much of the time during copulation they are held in the air. When the male extrudes the aedeagus, he rubs the tergite of the female pygidium to stimulate her to raise the pygidium and lower the last sternite in order that insertion can occur.

5.52.41 CURCULIONIDAE

There is information on mating behaviour in 14 genera but some have only very brief descriptions.

In Pantorhytes szentivanyi the sexes appear to be attracted to each other by visual means. Before copulation there is no courtship display; however, when mounted the male brushes the female prothorax with his antennae. The male spends a considerable time mounted on the female copulating intermittantly. Rarely the female is unreceptive and on these occasions, she kicks an unwanted mounted male with her hind legs. This may be correlated with incomplete maturation in the female. A male may attempt to quieten the female by palpating her dorsum. (Hassan, 1975).

Phyllobius pyri and P. artemisiae have been collected in close proximity, green P. pyri being common on trees and grey P. artemisiae in grass. A green female found on grass and placed with grey males from grass showed clear rejection behaviour when a male attempted to mount. The female extended her ovipositer, curling it downwards into the substrate to make male entry impossible, and at the same time rubbed the dorsal hind abdomen with the tibiae of both hind legs (R. T. Thompson, pers. comm.).

Lecato and Pienkowski (1970) report that males of Hypera postica are highly sexually active, spending 60% of their time mounted, while females are passive but usually receptive. The only indication of courtship in Microtharionus lareynii is a repeated series of antennal contacts. When mounted the male strokes the whitish setae on the female's pronotum and elytral bases with his antennae. If the female resists copulation the frequency and duration of the antennal stroking is increased, but is ceased during copulation (Kirkland & Goeden, 1978).

Mating is initiated in Stephanophorus punctiventris when the male meets a female and immediately mounts her (Eichler, 1951). The male may remain mounted for up to an hour before intromission. During introduction of the male genitalia into the vulva, the male strokes the sides of the female thorax with the vibrating brushes of his antennae. At the same time the male makes repeated thrusting movements of the genitalia as intromission occurs. During copulation the tip of the male rostrum is tapped on the intersegmental region between the pronotum and elytra.

In Pachytychius elongatus the female initially digs a hole, into which she plunges her head thereby raising her abdomen. During this time the male approaches and couples with her. Prior to mounting the male scratches the top of the ovipositor with his mandibles, then upon mounting the male pulls the setae on the female pronotum.

After a period of about 5 minutes the male genitalia are extruded and intromission occurs. After dismounting the male rubs the posterior edge of the female abdomen with his mandibles (Risbec, 1947).

In Anthonomus grandis (the ball weevil) copulation has been observed by Mayer & Brazzel (1963), Cross & Mitchell (1966) and Cross (1973). Males and females are usually in close proximity on cotton plants; however, males do not respond to females over a distance of 3 - 5 cm, but females were often attracted to males from a distance of about 30' in downwind positions. A windborne pheromone is thought to be produced by males, and possibly a weak secondary pheromone is released by females.

Females may perform elaborate tactile behaviour to induce males to mate; touching the male antennae, crawling over the male dorsum, sometimes assuming the male dorsal copulatory position and stroking his abdomen ventrally with her ovipositor. At this point the male would quickly reverse positions and mate with the female.

The female may resist copulation, if she has mated within 24 hours of the attempt. Resistance is exhibited by rapid swaying of the female body and moving the posterior abdomen dorsally to position the vagina vertically under the elytra to prevent insertion of the aedeagus.

Sexually active Hylobius abietis males always produce a series of acoustic signals when mounting a female. Receptive females respond by remaining stationary, but unreceptive females make jerky movements during which the male may be dislodged. Females were not observed to stridulate. Occasionally males will mount other males; however, the mounted male signals to the courting male and interrupts courtship. Acoustic signalling is thought to be the last stage in the behavioural sequence that leads to copulation, while

the preceding stages involve chemical and other stimuli. Close range recognition is thought to be at least partly based on chemical stimuli from antennal contact. Male signalling continues throughout mounting until genital contact is obtained. At this point tactile signals such as patting the female with the fore legs, comes into play.

Male to female stridulation aids in the discovery of whether a female is receptive. In receptive females the signals seem to inhibit locomotion. It is not known whether such signals also serve as a reproductive barrier.

Owing to the low intensity of the signals they do not seem to have the role of bringing the sexes together. Specific pheromones secreted by the females may have this purpose (Selandier & Jansson, 1977). Sounds are also produced by Conotrachelus nenuphor. Both sexes stridulate and either seems to be able to attract the other, although females have not been noted to stridulate until a male did so. Copulation does take place without being preceded by stridulation and males may continue to stridulate during copulation. The opposite sex responds to the stridulation by raising themselves and vibrating their antennae (Mampe & Neunzig, 1966).

Regarding secondary sexual characters the males of Attelabidae and Rhynchitidae have a unique endophallic transfer apparatus which shows a high degree of intra-specific stability (Hamilton, 1979). Sharp (1920) showed an exact correlation between male and female parts in Conotrachelus brevisetis. The transfer apparatus appears to fit directly the aperture of the spermathecal duct during copulation. The endophallic structures are thought to be analogous to the lateral lobes or parameres in other Coleoptera in that they serve to secure the endophallic sac within the female during copulation.

5.52.42 Mating Behaviour Review Discussion

The mating behaviour review aims to collate all the available information on such behaviour in the Coleoptera and then to correlate the types of signal used to communicate between males and females during courtship and mating with the general ecology of the group in question.

Details of mating position and the actual mechanics of mating have been omitted or are only briefly mentioned. The emphasis has been put on the types of signal employed, the sensory mode through which these signals operate and the significance of secondary sexual features, with regard to their divergence in closely related sympatric species.

The ecology of the group in question will, without doubt, affect the types of signal employed between sexes. Those groups predominating in aerial situations are more likely to use visual stimuli, acoustic signals and long range pheromones (e.g. Lampyridae, Scarabaeidae (Rutelinae), Cerambycidae, Cantharidae and Scolytidae). Those confined to substrate zones more commonly employ short range pheromones, close range acoustic signals and tactile signals (e.g. Staphylinidae, Silphidae, and some Carabidae). The ecology of the group further determines whether signals in closely related groups of species are similar or distinctly divergent. Where closely related species are generally allopatric, barriers to reproduction between them are likely to be of the "mate avoidance" type (Section 5.6); involving spatial, seasonal and other temporal differences which generally serve to keep potential males apart (e.g. Carabidae, Dytiscidae, and some Scarabaeidae). Where closely related species occur sympatrically signals exchanged between the sexes prior to and during mating are frequently divergent in order that dissortative mating is avoided.

The signals employed by the sexes have been loosely assigned

the function of "mate recognition" in the present review. This term is used in the broad sense to include signals involved in searching for and finding a potential mate, sex determination and behaviour at close quarters during which the receptivity of the female is determined along with stimulatory behaviour by the male carried out immediately prior to intromission. This therefore includes the "specific mate recognition features" which are structures thought to be used as species specific signals exchanged at close quarters (e.g. peg patterns of Philonthus).

The types of signal fall into four categories, chemical, visual, acoustic and tactile.

Chemical signals include short and long range sex attractants which serve to bring the sexes together, the latter are most often employed by aerial species (e.g. Scolytidae) and are usually non-specific, more specific signals being employed once the potential mates are within close range (e.g. Anobiidae (Ptilinus and Lasioderma), Silphidae (Nicrophorus), Lucanidae (Lucanus), Scarabaeidae (Rutelinae Popillia, and Macroductylis), Buprestidae (Agrilus), Elateridae (Ctenicera), Drilidae (Drilus), Cantharidae, Dermestidae, Tenebrionidae (Tenebrio), Scolytidae, Curculionidae (Anthonomus)).

Close range, or contact, chemoreception is almost universal throughout the Coleoptera. It is not known how far such chemicals are species specific; but undoubtedly in many cases they are and in some this has been proved (e.g. Aleochara curtula (Staphylinidae), Trechus (Carabidae) and possibly also Dytiscus (Dytiscidae), Olophrum (Omaliinae, Staphylinidae), Cyphon (Helodidae) Scarabaeini etc., Pteroptyx and Pyrophorus (Lampyridae), Trogoderma (Dermestidae), Melyridae, Lytta (Meloidae), Cerambycinae, and Lepturinae (Cerambycidae)).

Species which find potential mates by visual means are generally aerial. Colour dimorphism is used by males of Cotalpa puncticollis (Scarabaeidae) and other ruteline species which

aggregate on flowers or foliage. Visual location following chemosensory stimuli is used in Pseudocotalpa giulianii (Buprestidae). Female luminescence is utilised in the Elateridae and Phengodidae, and long distance location and size discrimination of females is achieved by male Rhagium (Cerambycidae).

Acoustic signals in the Coleoptera are generally exchanged at close quarters in water living and substrate species as well as a few aerial species. In many cases stridulation occurs while in the mounted position: in some cases this is achieved by stroking the female body*, (e.g. Carabus nemoralis (Carabidae), Haliphus wehnckeii (Halipilidae), Lucanus and Platycerus (Lucanidae), Passalidae, Bolitotherus (Tenebrionidae), Priomus (Cerambycidae)). Premating stridulation, which may also continue in the mounted position, occurs in Berosus, Hydrobius and Spercheus (Hydrophilidae), Passalidae, Buprestis rustica (Buprestidae), Hylastes rugipennis, Dendroctonus, and Ips, (Scolytidae), and Conotrachelus (Curculionidae). In Hylobius (Curculionidae) stridulation while mounting is thought to inhibit locomotion in receptive females. There is potential for divergence of acoustic signals in closely related sympatric species; however, there is little information regarding the specificity of such signals. Only in the Hydrophilidae have the signals of sympatric and allopatric species been compared, with the result that the signals of sympatric species show marked differences, whereas those of the allopatric species do not.

Tactile signals, generally of a non-specific type, are used by most species during courtship as part of a necessary sequence of stimuli that lead to intromission and include antennation, palpation and leg rubbing. The potential for specificity in different patterns of tactile behaviour have been studied in detail in the Meloidae. In the Meloinae, which only mate once before oviposition

and where there is a locking mechanism, there is an elaborate courtship display involving tactile stimuli.

The Nemognathinae which mate several times before oviposition and lack a locking mechanism have a very simple courtship. In the genus Pyrota (Lyttini) species are strictly phytophagous and host specific and the mating site corresponds to the feeding site. Here there is no preliminary signalling, only tactile stimuli once the pair are in the mating position. It has been shown that when sympatric species occur together there is an ethological divergence in courtship. Tactile displays are replaced almost completely by chemosensory stimuli in the Epicautina.

Tactile signals involving structures which may be recognition features tend to be employed only in those groups where reproductive isolation is not of the mate avoidance type and where closely related species are found together, for example many Staphylinidae and Pterostichus (Carabidae). In the Carabidae, sister species very frequently appear to be allopatric or, if inhabiting the same general area, have non-overlapping niches. The opportunities for species specific behaviour during mating is limited by a very simple pattern of courtship. Specific mate recognition systems may include specific tactile signals deriving from a specific pattern of movements as in many Coleoptera, but only in a few cases might differences in male structure form part of the signal, e.g. some Pterostichus spp. where a tubercle on the male seventh sternite is rubbed over the female elytra. There may be small differences in shape of the tubercle but the pattern of movement employed and the presence or absence of such a structure in closely related species may provide potential for a reproductive barrier.

In contrast the Staphylinidae, which fulfill a very similar role to the Carabidae in substrate zones, are frequently found sympatrically

and as illustrated elsewhere (Section 4) structures of a putative tactile recognition type commonly occur in such species.

In general, the literature on mating behaviour only records the presence or absence of types of signals employed between males and females. In very few cases are sympatric and allopatric species pairs studied and compared. The potential for divergence is clear in signals produced by chemical, acoustic and tactile means where closely related species occur sympatrically. This theme is continued in the following section while going onto consider the aspects of recorded cases of cross mating and hybridisation in relation to premating reproductive barriers.

5.6 Cross Mating and Hybridisation

Premating reproductive barriers between closely related species are not always fully effective in nature and this is demonstrated by records of cross-matings and hybridisation. For Coleoptera, such records have been collated from the literature, along with records for hybridisation under laboratory conditions (Appendix 1).

The list has been compiled from data collected primarily from the Zoological Record 1899-1974 with other varied sources.

The most recent nomenclature has been adopted, derived from catalogues in the BMNH based upon the *Coleopterorum Catalogus series* (publ. W. Junk). Consequently generic and specific names may differ from those used originally. Only 14 families are represented in the list in all, the majority of examples are of Carabidae and Chrysomelidae. The other families included are Carabidae, Dytiscidae, Hydrophilidae, Staphylinidae, Scarabaeidae, Buprestidae, Elateridae, Cantharidae, Dermestidae, Coccinellidae, Cerambycidae, Bruchidae, Chrysomelidae, and Curculionidae. Most instances relate to closely related pairs of species. Some observations, however, relate to cross-matings between more distantly related species, sometimes of different families. As far as is known all the species pairs listed are sympatric in the field; those with a parapatric distribution (*) are regarded by some authors as subspecies or geographical races. Although records of cross-matings and hybrid production are included in the same list, the conclusions with regard to the operation of premating reproductive barriers which may be drawn from these differ.

In most species pairs included in the list premating reproductive barriers are likely to be "ecological" (Mayr, 1963) involving spatial, seasonal, and other temporal differences which generally

serve to keep potential mates of the different species apart.

Such barriers are termed "mate avoidance" by Hammond (in press^b).

Generally, very closely related species of the Carabidae and Dytiscidae do not occur together and signals serving to bring the sexes together, or those exchanged at close quarters, may not be species specific. The production of chemicals which may be species specific have been detected only in species of Trechus (Leitner, 1943) and specific olfactory signals have been suspected in aquatic Dytiscidae (Smith, 1973).

Closely related species of Scarabaeidae are reproductively separated by spatial, seasonal and other differences in mating times. However, there is evidence of cross-mating and hybrid production in certain species under laboratory conditions (Ritcher, 1958). Female sex attractants are thought to exist in some Phyllophaga spp., but it is not known whether these are species specific (Wojcik, 1969a&b). In other species marked differences in the sclerotised apical genital processes of both sexes would act as a mechanical barrier to cross-mating if the ecological barriers were broken down (Ritcher, 1958). Such differences may be involved in tactile signalling.

Host specificity may operate as an effective premating barrier to reproduction only when the mating site is associated with the feeding site e.g. many Chrysomelidae, some Curculionidae, Cerambycidae. In the Buprestidae where Agrius spp. are host specific as larvae, adult female A. horni is known to produce air borne attractants and it is suspected that species specific acoustic signals are produced (Carlson & Knight (1969) and Dutt (1969)).

Other reproductive barriers are operative in closely related species of Helophorus (Hydrophilidae) which are normally separated

by differences in habitat. Angus (1970) investigated pre and post-mating barriers under laboratory conditions in H. flavipes F., H. obscurus Muls. and H. strigifrons Thoms. and these were observed to operate via hybrid sterility. Unmated females also lay eggs in the presence of males belonging to a different species.

Post-mating reproductive barriers are operative where mate avoidance by ecological separation is not employed. This is the case where, prior to mating, males and females of some families aggregate on flower heads of Compositae and Umbelliferae (e.g. Cantharidae, Coccinellidae, Cerambycidae, Chrysomelidae and Curculionidae, in some species of which there is specificity of feeding site in the larvae). A common mating site of this type may lead to a breakdown of any existing premating barriers but in most cases any hybrids produced are infertile.

Other barriers in operation in the Cerambycidae, Curculionidae and Dermestidae include temporal and spatial separation, visual discrimination, pheromone production and stridulation but the specificity of these is unknown.

Some apparent anomalies appear in the list. This includes the inter-familial or inter-generic cross-matings which may be readily observed with males of cantharid species since they are sexually very active and indiscriminate in their choice of partner. Species specific signals may be employed by the male during courtship; however, it is the female reaction to such signals which is important.

In the Cantharidae and the Staphylinidae (discussed below), the females are coy and reproductive barriers are partially based on the lack of response from a female which has not received an appropriate signal.

Cross mating in the Staphylinidae is represented by only two examples:-

Quedius scintillans Female x Heterothops dissimilis Male

(Donisthorpe, 1928): Quedius scintillans does not have any closely related species with which it is syntopic and the male secondary sexual features are not striking in the context of the genus as a whole. Also Heterothops males do not exhibit striking secondary sexual features and the lateral lobe is absent. The pair were observed in copula only and it is not known whether effective genital linkage was achieved. Quedius females are known to respond only to a specific set of signals exchanged between the sexes at close quarters (Section 5.2.8 & 9); but, under laboratory conditions interference in premating barriers is likely to occur and in these circumstances it is feasible that such a cross-mating could occur.

Weber (1921) does not state which is the male or female in the cross-mating between Bolitobius analis and Tachyporus chrysomelinus. If the arrangement of stout setae on the male abdominal sternites and the shape of the median lobe apex, which are characteristic of individual species closely related to B. analis (Section 4), are part of a tactile signalling system involved in specific mate recognition, then it seems unlikely that a female B. analis would accept a male without these features. Tachyporus spp. do not possess any elaborate secondary sexual features.

There is little detailed analysis of the operation of reproductive barriers between closely related species in the literature. A well documented example is that of Diabrotica virgifera and D. longicornis barberi (Chrysomelidae, Krysan & Guss, 1978). The pair are closely related and sympatric, frequently occurring at the same time in cornfields in the central United States. A highly effective reproductive barrier is operative in the field and laboratory between these species and is probably ethological, since in male choice experiments only conspecific matings occurred;

however, if the species were kept together over a longer period of time, some interspecific mating occurred. Pre-mating barriers, in the field, included dissimilar feeding habits and daily activity patterns. A post-mating barrier is thought to exist since egg hatch from interspecific crosses was lower than from conspecific pairings. There is no evidence for the occurrence of inter-breeding in nature.

CONCLUSIONS

The difference between records of cross-matings and production of hybrids has already been mentioned. Observations of cross-matings bear little information regarding the stage to which coupling was achieved. In some cases mating may proceed to insemination while in others an effective genital linkage may not even be made.

Data derived from laboratory studies should be regarded critically also, since species may be brought together which in the field do not meet; or if they do, barriers in operation in the field may easily be interfered with under such conditions.

It is concluded that species in which putative tactile recognition devices (and other species specific signalling systems which may operate at close quarters) are not present in the list. This may be regarded as circumstantial evidence that the putative tactile recognition devices function in this way and that specific signals exchanged at close quarters provide particularly effective reproductive barriers.

SECTION 6

VARIATION IN MORPHOLOGICAL CHARACTERS OF TWO 'PARTIALLY'
SYMPATRIC SPECIES, WITH PARTICULAR REFERENCE TO THE MALE
GENITALIA IN DIFFERENT GEOGRAPHICAL LOCATIONS

6.1 Introduction

It has been suggested that in cases where two closely related sympatric species overlap for part of their distribution mate recognition signal system "dialects" may occur. These occur beyond the area of overlap, when selection pressure to limit the variation between populations is relaxed.

To investigate whether known variation in genital characters, thought to be involved in species specific signalling, conforms to this pattern the geographical variation of a variety of morphological characters has been examined in males of two large staphylinids, Quedius mesomelinus Marsh. and Q. maurus Sahlb. External characters are compared with those of the male genitalia.

The two species are closely related and are of very similar appearance, the females being very difficult to distinguish, and the males only readily separable after dissection of the genitalia. Large samples of both species reveal a notable difference in overall body size, Q. maurus being the smaller of the two.

Distribution

Q. mesomelinus has a very broad distribution (Horion, 1965) which includes the Palaearctic, Iceland, Greenland, North and South America, Australia and New Zealand. Q. mesomelinus is reputedly cosmopolitan but mainly in cool temperate climates. The native

distribution of the species is in the Palaearctic only, its occurrence elsewhere represents secondary introductions (Smetana, 1971).

In comparison, Q. maurus is restricted in distribution to northern and central Europe, with northern limits in Trondheim, Norway, south Lapland, Ostrobothnia, Finland, and the Scottish highlands, and southern limits of northern Spain, the Pyrenees, Toscana, Italy, Yugoslavia and the Caucasus, (Horion, 1965) (Fig. 6.1) Lindroth, 1960, Bordoni, 1974a & b, Outerelo, R. pers. comm.). The precise distribution of Q. maurus is not well documented; in the present study specimens have been seen from Germany, Czechoslovakia, Italy and Britain (England and Scotland).

Habitat

Both share similar primary habitats, as woodland species associated with fungus and rotting wood. Q. maurus remains restricted to this type of habitat while Q. mesomelinus has broadened its habitat to include synanthropic habitats, (rotting vegetation, compost heaps, etc.) caves and underground situations such as animal burrows, (Smetana, 1971).

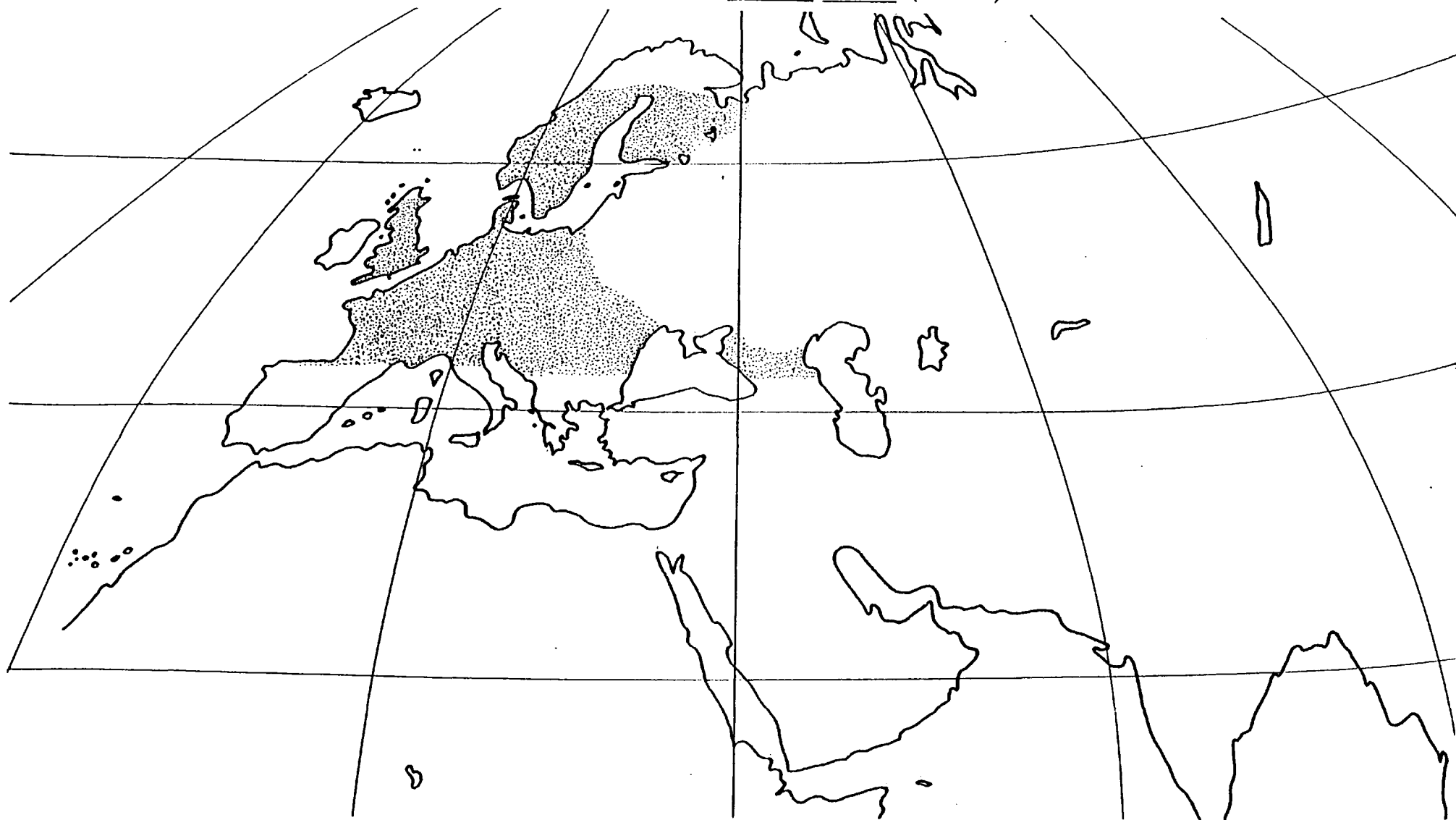
Life History

Little is known of the life histories of either species. Kasule (1968) and Frank (1968) have studied the life histories of other Quedius species, Q. fumatus (Steph.), Q. fuliginosus (Grav.), Q. melichimus (Grav.), Q. picipes (Mann.), Q. lateralis (Grav.) and Q. curtipennis Bernh.

Horion (1965) records Q. mesomelinus as being abundant throughout most of the year, particularly from April to October, and larvae and pupae were collected from moles nests in Denmark at the end of August.

Data from Chiswick House (Hammond, pers. comm.) indicates

Fig.6.1 Map to show the extent of the known distribution of Quedius maurus (shaded).



that Q. mesomelinus adults occur from January to May and then July December, with peak captures in April to May and November. Larvae occur from January to March, with a peak in February to March. Pupae have been collected during May, and teneral adults in July. Larvae have also been collected in April, May, June, July and teneral adults in April. This may indicate that there are two generations per year.

In the present study, larvae of Q. mesomelinus were collected from a garden compost heap in January and reared at 20°C and 16 hr/24 hr light regime (Section 2.2). The larvae pupated 12 - 26 ($\bar{x}=16.36 \pm 1.16$ (SE) days after collection, although allowance should be made for age differences in the larvae, and adults emerged 9 - 16 ($\bar{x}=12.42 \pm 0.532$ (SE) days after pupation. There was no obvious difference in the development time of the two sexes (Table 6.1).

Morphological Variation

Korge (1961) investigated Q. mesomelinus populations in Europe and found that the median and lateral lobes of the male genitalia were surprisingly variable, and that this condition occurred among individuals of the same population. Korge also described four subspecies of Q. mesomelinus and one new species, to account for apparently isolated populations which, while externally similar, other features exhibited more extreme forms of variation, particularly in the genitalia. The form of the genitalia for each population remained constant.

The subspecies and species proposed were:-

1. Q.m. mesomelinus Marsh; (Fig. 6.2): dominant geographical form.
2. Q.m. kraussi Penecke (Fig. 6.3a-c): from south-eastern Europe; caves and mountains in Yugoslavia.

TABLE 6.1 Data concerning the development of *Q. mesomelinus* in
laboratory conditions

<u>Number of days from</u> <u>collection to pupation</u>		<u>Number of days from</u> <u>pupation to adult</u> <u>emergence</u>		<u>Number of days from</u> <u>emergence to death</u>
1	14	11	♀	-
2.	12	-		pupa damaged
3.	14	12	♂	-
4.	14	12	♀	-
5.	14	12	♂	-
6.	14	15	♀	63
7.	14	15	♀	-
8.	17	12	♀	-
9.	17	12	♂	50
10.	17	13	♂	123
11.	22	9	♂	-
12.	22	16	♀	-
13.	22	14	♀	87
14.	24	-		pupa damaged
15.	26	12	♀	-
16.	3	9	♂	46
17.	15	adult <u>Codrus</u> sp. Hymenoptera, Proctotrupoid) emerged from <u>Quedius</u> larva		
18.	15			
19.	15			

$\bar{x}$	16.36	$\bar{x}$	12.42
SE	1.160	SE	0.532
n	19	n	14

Fig.6.2 Male genitalia of Quedius; Q.mesomelinus, a) median lobe lateral view, b) median lobe ventral view, c) lateral lobe, d) median and lateral lobe lateral view.

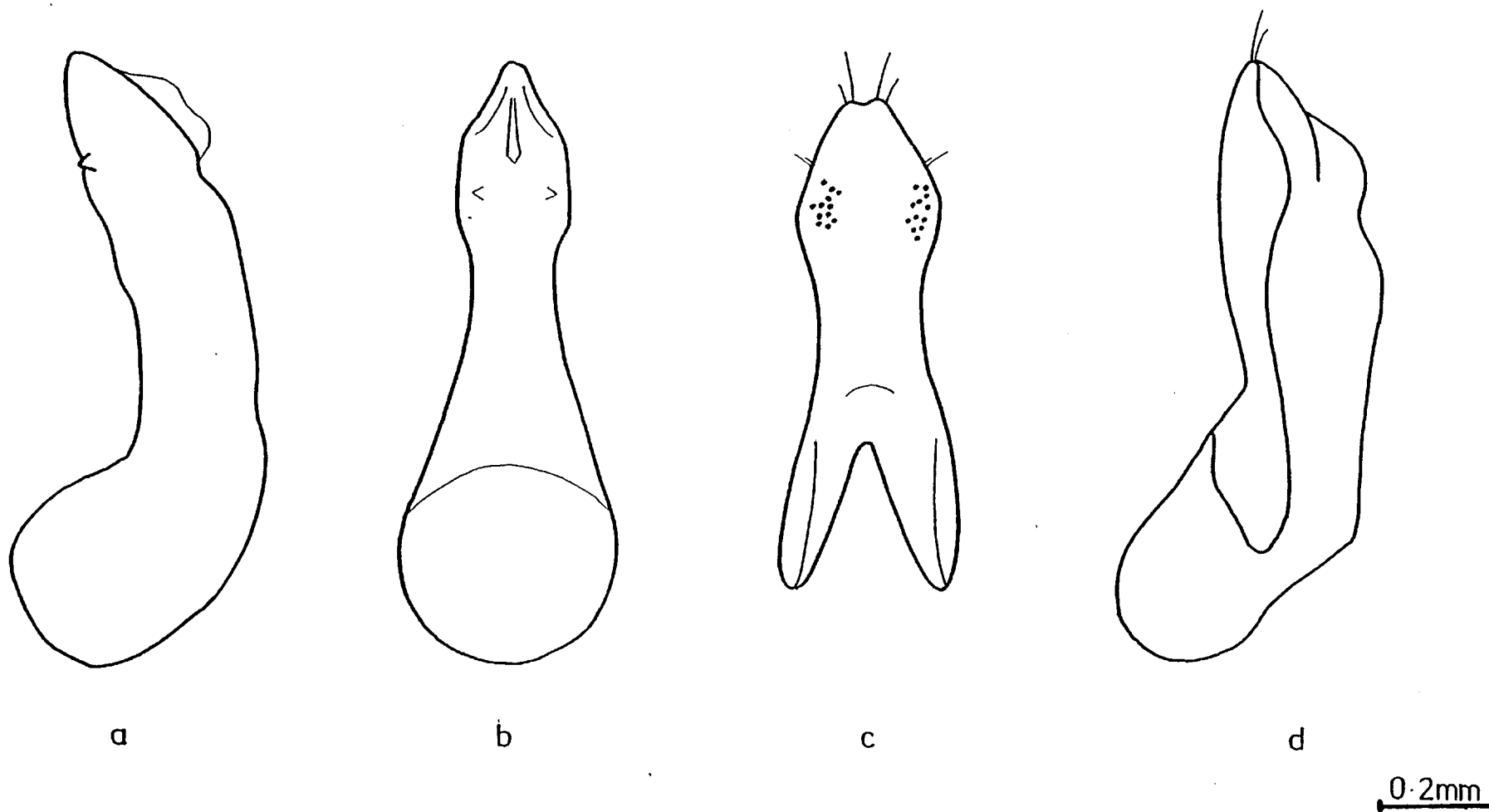
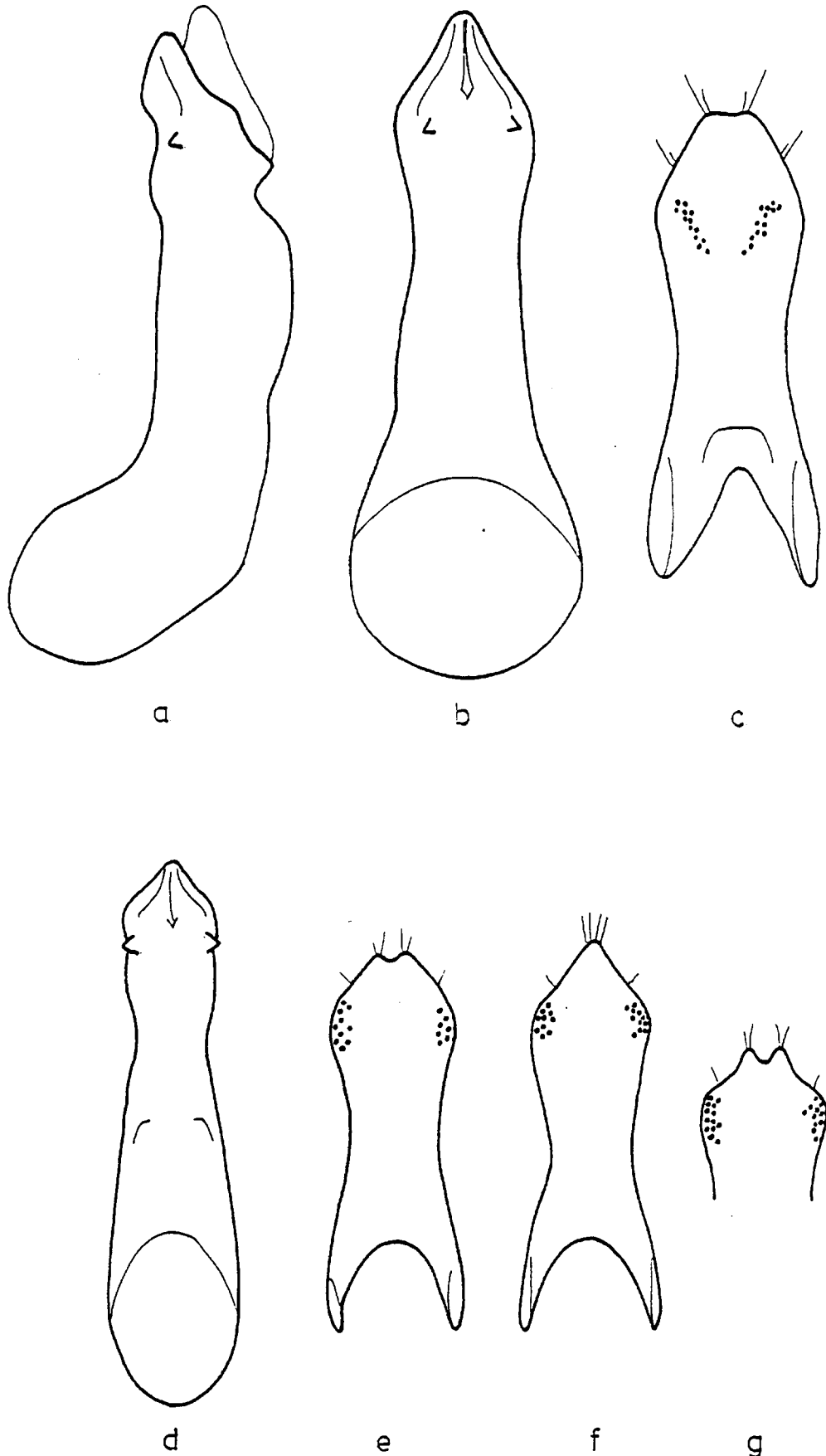


Fig.6.3 Male genitalia of Quedius; a-c) Q.m.kraussi, d-f) Q.m.silensis, g) Q.m.fiorii. a) median lobe lateral view, b) median lobe ventral view, c) lateral lobe, d) median lobe ventral view, e-g) lateral lobe.



0.2mm

3. *Q.m. silensis* Fiori (Fig. 6.3d-f): from southern Italy.
4. *Q.m. fiorii* Korge (Fig. 6.3g): from central and northern Italy, in caves.
5. *Q. skoraszewskyi* Korge (Fig. 6.4d-f): from eastern and south-eastern alpine areas, a high altitude species.

Korge suggested that the great variation around the Adriatic sea indicates the area of origin of *Q. mesomelinus*. He believed that in the post-glacial era the variability continued to be lost as North and Central Europe were colonised.

During the present investigation attention has been paid to the two undoubtedly good species, *Q. mesomelinus* and *Q. maurus*, (Fig. 6.4a-c), to examine the incidence of variability in relation to geography in these partially sympatric species. The subspecies and new species proposed by Korge have also been examined in an attempt to discern whether these populations deserve specific or subspecific status, or, if they are to be regarded as peripherally isolated geographical races.

6.2 Materials and Methods

Material from the following Collections has been studied:-

British Museum (Natural History) London.

Zool. Forschungsinstitut and Museum Alexander Koenig, Bonn.

Institut Royal des Sciences Naturelles de Belgique, Brussels.

Universidad Complutense, Madrid - Dr. R. Outerelo.

Biosystematics Research Institute, Ottawa - Dr. A. Smetana.

Université Paul Sabatier, Toulouse - H. Coiffait.

Természeti idományi Museum, Budapest.

Museo Civico Di Storia Naturale, Verona.

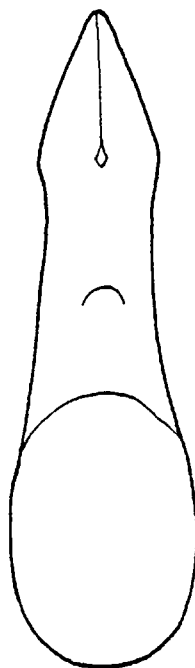
Chicago Field Museum.

Fig.6.4 Male genitalia of Quedius; a-c) Q.maurus, d-f) Q.skoraszewskyi.

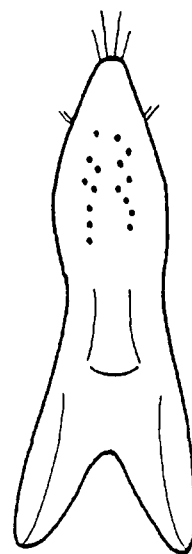
a&d) median lobe lateral view, b&e) median lobe ventral view,
c&f) lateral lobe.



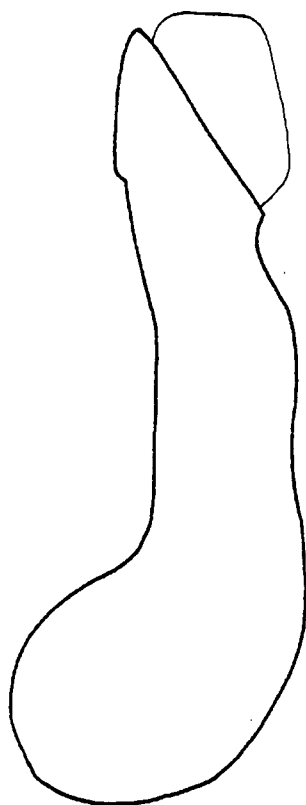
a



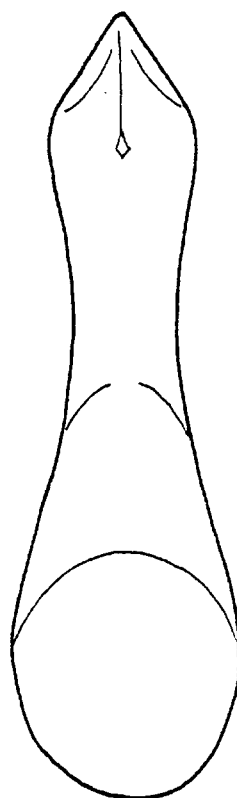
b



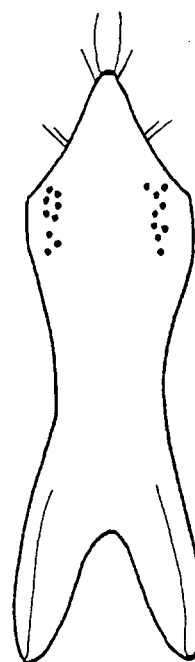
c



d



e



f

0.2mm

Number of individuals examined

152 individuals of Q. mesomelinus s.str.

20 individuals of Q.m. kraussi

2 individuals of Q.m. fiorii

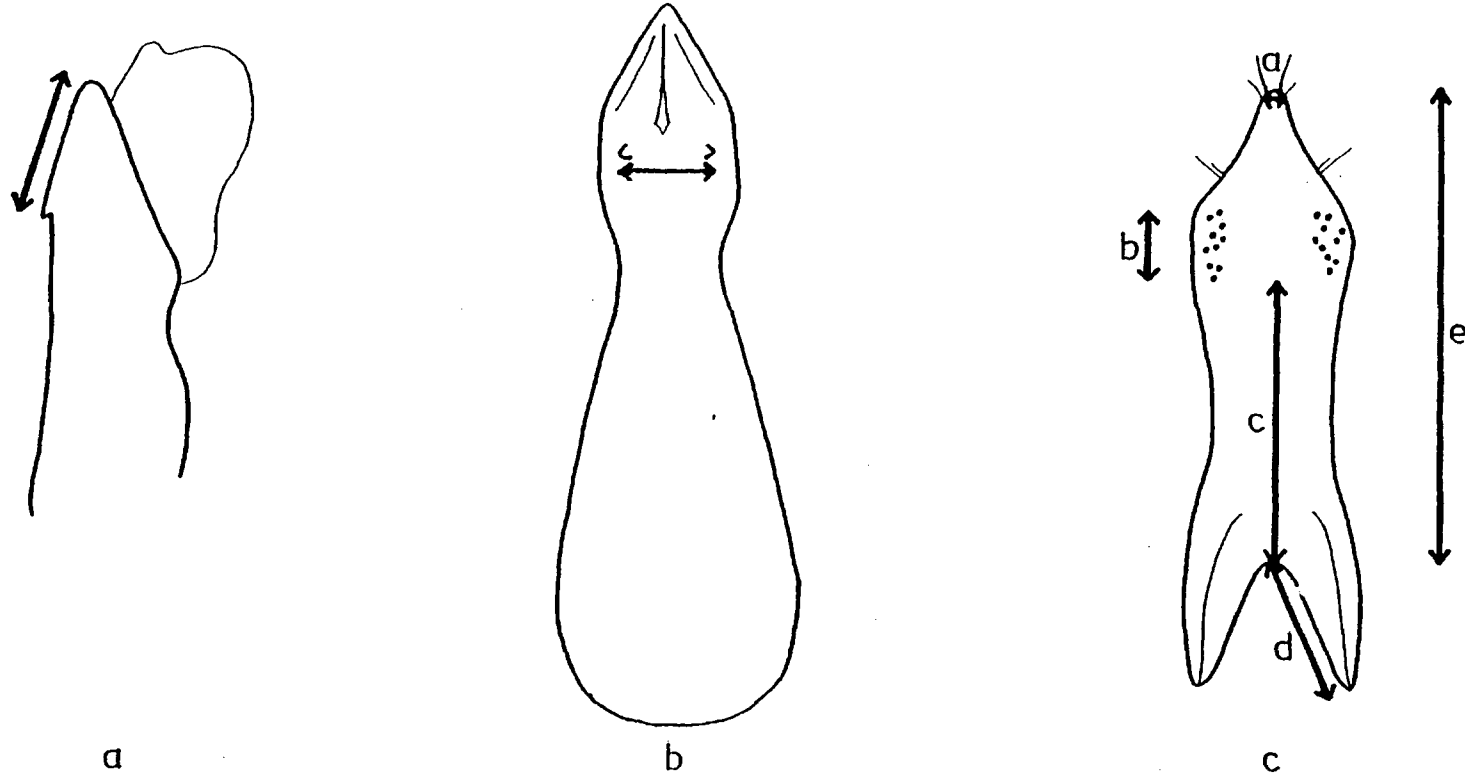
3 individuals of Q.m. silensis

Characters examined

23 characters were measured using an eye-piece graticule fitted to a Wild M5 microscope, calibrated with a Leitz stage micrometer and include:-

1. Pronotum length - in mid-line
2. Pronotum breadth - at widest point
3. Elytron length - from highest point of shoulder to extreme apex
4. Elytron breadth - at widest point across one elytron
5. Median lobe length
6. Distance between two apical projections on median lobe
(abbreviated < >) (Fig. 6.5b).
7. Length apical strut median lobe (Fig. 6.5a)
8. Breadth median lobe apex - at widest point
9. Breadth lateral lobe apex - (Fig. 6.5c(a)) between 2 external setal sockets.
10. Length lateral lobe - (Fig. 6.5c(e))
11. Breadth lateral lobe - (Fig. 6.5c) at widest point at peg pattern level.
12. Length basal piece lateral lobe - (Fig. 6.5c(d))
13. Length base of lateral lobe to start of peg pattern (Fig. 6.5c(c))
14. Length peg pattern - (Fig. 6.5c(b))
15. Number of pegs - left side of lateral lobe
16. Number of pegs - right side of lateral lobe
17. Length/breadth pronotum
18. Length/breadth elytron
19. Pronotum length/median lobe length

Fig.6.5 Diagram to illustrate features of Quedius measured; a) length apical strut median lobe, b) distance between two apical projections on median lobe (abbreviated $\langle \rangle$), c) a- breadth lateral lobe apex between two external setal sockets, b- length peg pattern, c- length base of lateral lobe to start of peg pattern, d- length basal piece lateral lobe, e- length lateral lobe.



20. Pronotum length/lateral lobe length
21. Lateral lobe length/peg pattern length
22. Median lobe length/lateral lobe length
23. Length-apex of scutellum to apex of elytra at mid suture.

For 21 individuals of Q. maurus and 29 individuals of Q. skoraszewskyi 22 of the above characters were measured since character 6 is absent in these two species.

External characters were measured in the dry state, and genital characters were dissected and measured in glycerine. All measurements were converted to millimetres.

Results were statistically summarised using a computer programme by R. G. Davies, Imperial College. This gives for each set of data: mean, standard error, variance, standard deviation coefficient of variation, minimum and maximum measurement, range and sample size.

Data was grouped into 13 categories, to enable comparison of species in different locations.

1. Q. mesomelinus - 20 individuals from one population near Pontrilas, Herefordshire, England.
2. Q. mesomelinus - 43 individuals. All British locations only (1 + 2)
3. Q. mesomelinus - 124 individuals. European locations only (1 + 2 + 3)
4. Q. mesomelinus - 13 individuals. Extra-European locations only.
5. Q. mesomelinus - 137 individuals. All locations except Falkland and Shetland Islands (1 + 2 + 3 + 4)
6. Q. maurus - 11 individuals. British locations only.
7. Q. maurus - 21 individuals. All European locations (6 + 7)
8. Q.m. silensis - 3 individuals.
9. Q.m. fiorii - 2 individuals.
10. Q.m. kraussi - 20 individuals.
11. Q. skoraszewskyi - 29 individuals.

12. Q. mesomelinus - 16 individuals. Falkland Is.
13. Q. mesomelinus - 3 individuals. Shetland Is.

Locations of all individuals were mapped onto a Universal Transverse Mercator grid map using a computer programme by C. A. Russell, M.O.D., to convert longitude and latitude into the equivalent rectangular co-ordinates of the U.T.M. projection, (Map 1).

Small sample numbers of Q.m. silensis and Q.m. fiorii are due to unawareness of existence, undercollecting and apparent indistinguishability from other Q. mesomelinus.

6.3 Results

A computer printout of the full and summarised data is in Appendix 2.

1. Comparison of the variation, measured by the coefficient of variation in each character.

In each category the coefficients of variation for each character were compared graphically (Fig. 6.6).

2. Comparison of means and ranges for each character

For each character the mean and range of measurements is plotted against their species category, in order to compare actual ranges of variation and the position of that range indicating any overlap between categories (Figs. 6.7-6.20).

3. Comparison of species using bivariate plots.

- a) length/breadth pronotum / length median lobe (Figs. 6.21-6.23).
- b) median lobe length/lateral lobe length (Figs. 6.24-6.26)
- c) lateral lobe length/peg pattern length (Figs. 6.27-6.29).

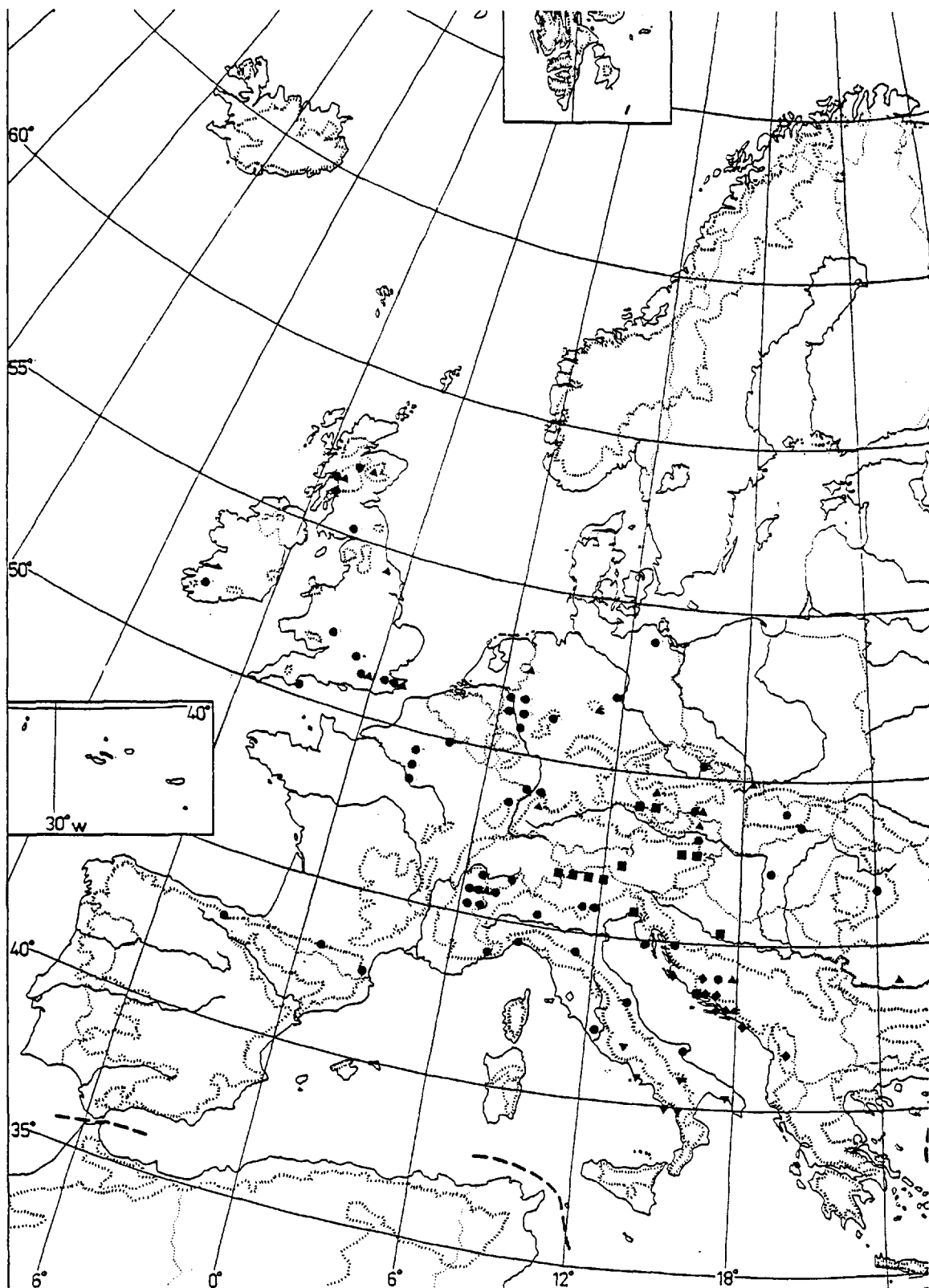
4. Geographical trend in median lobe length

Comparison of median lobe lengths across Europe, from northern Britain to southern Europe (Figs. 6.30 & 6.31).

5. Correlation between median lobe length and pronotum length

Map 1. Palaearctic locations of individuals of Quedius measured.

- mesomelinus ●
- maurus ▲
- skoraszewskyi ■
- kraussi ◆
- silensis ▼
- fiorii ◇



6.4 Discussion of Results

Owing to the sparser collecting and therefore small collections of Q.m. silensis and Q.m. fiorii in the locations where these "varieties" occur, only 3 and 2 individuals respectively were seen and measured. Results for these are consequently not a true reflection of the situation in their populations and therefore they will not be subject to the same analyses as the other categories, but will be discussed where relevant.

6.4.1 Comparison of the variation, measured by the coefficient of variation in each character

Graphical comparison of coefficients of variation in each character (Fig. 6.6) reveals that the most variable character in all cases is the breadth of the apex of the lateral lobe.

At the apex are situated four setae and the range of variation in this character in Q. mesomelinus is from a very tapered apex with all four setae at the tip, to a broad apex deeply indented in the mid-line with two setae on each side of the emargination (Fig. 6.2). All variations between these two extremes may be exhibited within one population alone. The apex of the lateral lobe in Q. maurus varies only in breadth, the tip never being medially emarginate. It is interesting, however, that European Q. maurus exhibits greater variation in this character than Q. mesomelinus, owing to breadth variation alone.

Table 6.2 lists for each category the first three most constant and most variable characters, omitting the apex breadth of the lateral lobe which has been discussed. It is significant that the most variable characters in all cases involve the peg setae which are situated on the surface of the lateral lobe which faces the median lobe. It has been hypothesised that the peg setae occur in specific patterns and form part of a sequence of events in the recognition of a conspecific male during mating. It is therefore somewhat surprising that this character should account for so much variation.

Fig.6.6 Histogram to show the comparison of the variation, measured by the coefficient of variation, in each character in Quedius species.

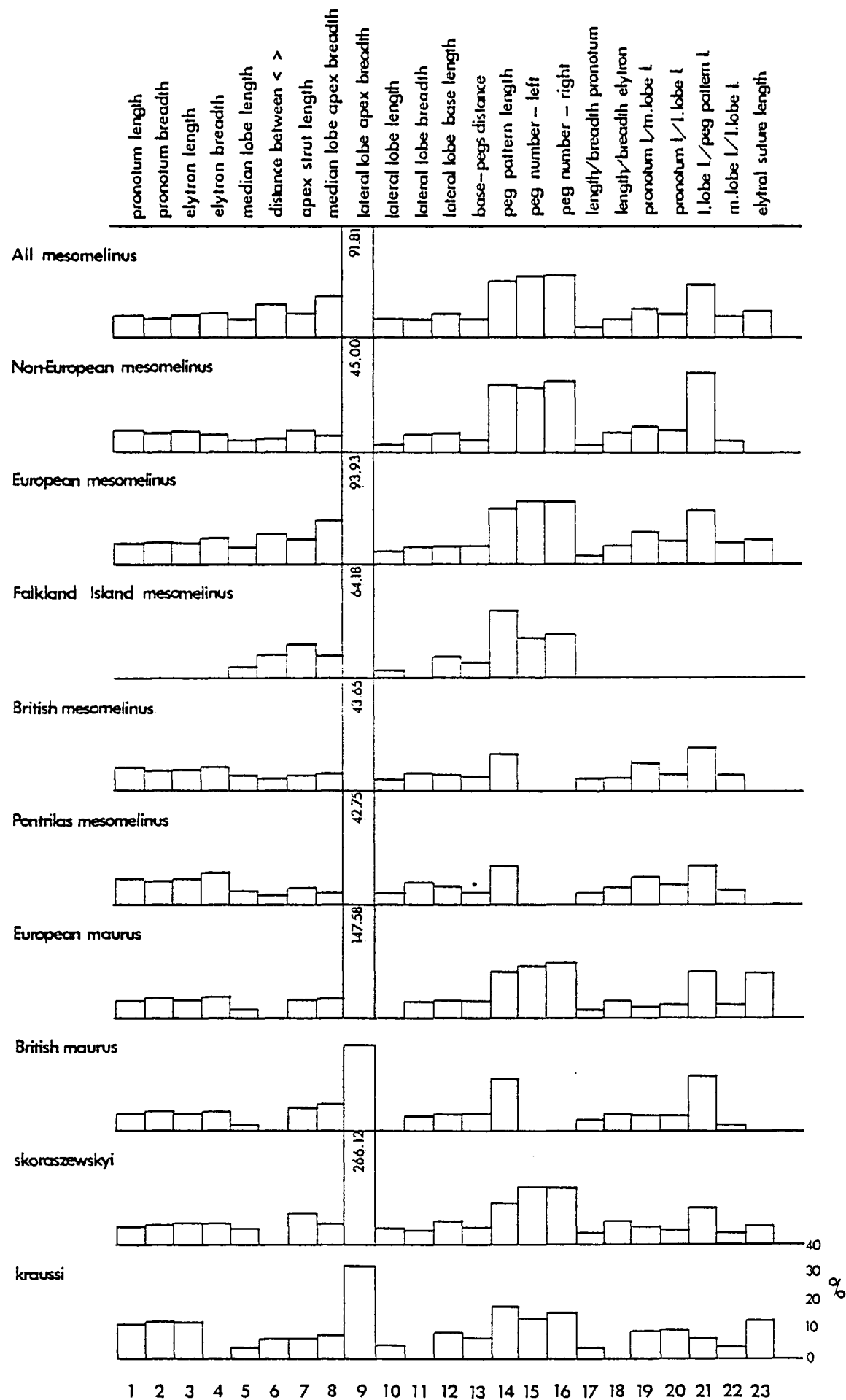


TABLE 6.2 List of the first three most constant and most variable characters in the different groups of species

	CONSTANT	VARIABLE
All <u>Q. mesomelinus</u>	length/breadth pronotum length/breadth elytra distance:lateral lobe base-pegs	peg number (right) peg number (left) lateral lobe length/peg pattern length
Extra-European <u>Q. mesomelinus</u>	length/breadth pronotum lateral lobe length elytron length	lateral lobe length/peg pattern length peg number (right) peg pattern length
European <u>Q. mesomelinus</u>	length/breadth pronotum lateral lobe length median lobe length	peg number (left) peg number (right) lateral lobe length/peg pattern length
British <u>Q. mesomelinus</u>	lateral lobe length length/breadth pronotum length/breadth elytra	lateral lobe length/peg pattern length peg pattern length elytron breadth

TABLE 6.2 (continued)

	CONSTANT	VARIABLE
Single locality <u>Q. mesomelinus</u>	distance < > lateral lobe length median lobe length	lateral lobe length/peg pattern length peg pattern length elytron breadth
European <u>Q. maurus</u>	length/breadth pronotum median lobe length/lateral lobe length median lobe length	peg number (right) peg number (left) lateral lobe length/peg pattern length
British <u>Q. maurus</u>	median lobe length/lateral lobe length lateral lobe length median lobe length	lateral lobe length/peg pattern length peg pattern length median lobe apex breadth

TABLE 6.2.

(continued)

CONSTANT

VARIABLE

Q. skoraszewskyi

length/breadth pronotum

peg number (left)

median lobe length/lateral lobe
length

peg number (right)

lateral lobe breadth

lateral lobe length/peg pattern length

Q. m. kraussi

length/breadth pronotum

peg pattern length

median lobe length/lateral lobe
length

peg number (right)

lateral lobe length

peg number (left)

The peg pattern as a whole is species-specific. The components which make up the pattern have quite a large variance so long as the signal contained in the whole pattern is not altered. Thus, the numbers and precise position of the individual peg setae are not critical provided the overall pattern remains the same.

Meristic analysis of the peg patterns, here, using numbers of pegs and length of peg pattern reveals the variability within the pattern, but does not show that the pattern as a whole remains constant in each species. Further analysis of the pattern to discern which part of it is important in relating information to the female and an idea of the tolerance levels of variation in the components is more appropriate and is discussed later.

In considering nine of the thirteen categories in which the species were grouped, the characters which remain most constant involve 8 of 23 analysed (Table 6.2). Of these the distance from the base of the lateral lobe to the start of the peg pattern, the distance $< >$, and the breadth of the lateral lobe each occurred only once out of the nine categories and length/breadth elytra twice. The most significant characters are the length/breadth pronotum which in 6/9 cases is the most constant character and in 7/9 cases one of the two most constant characters. In 7/9 cases the length of the lateral lobe, and in 4/9 cases the length of the median lobe and median lobe length/lateral lobe length fall within the first three most constant characters.

It might be expected that the genitalia would remain one of the most constant features with small tolerance for variation because of the possibility of incompatibility between conspecific males and females, particularly if aspects of the male genitalia form part of a specific mate recognition system. Other external characters of the body would have no corresponding requirement to remain so

rigidly constant and may therefore be subject to geographical variation. However, the body proportions represented here by length/breadth of pronotum, are likely to remain fairly constant because while the overall size of an insect may vary, the shape and proportions would remain the same.

Hammond (1972b) has shown, in species of British Sepedophilus Gistel, that estimated variation in pronotum and elytral characters was of the order of 10-15% and in the genitalia (measured by length only) 2-3%.

In the present study the coefficient of variation in pronotum and elytral characters was generally 6-10% and in the genitalia, taking into account lengths of the median and lateral lobes only, 1-6%.

The amount of variation throughout the rest of the body is very similar in all the categories. Pronotum length, breadth and elytral length exhibit similar levels of variation while elytral breadth was more variable in 6/9 categories. The median lobe length in all cases showed greatly reduced variation as in most cases did the lateral lobe length, although this was not as pronounced. Similar trends are exhibited by all further characters.

British Q. mesomelinus as a whole, and those from a single locality in Britain, are very similar in levels of variation. Continental European Q. mesomelinus generally exhibit greater variation in most characters. High levels of variation are notable in Falkland Island specimens, where the whole population must be small, particularly when compared with Britain.

British and Continental European Q. maurus are very similar: Q. skoraszewskyi exhibits comparable levels of variation with Q. mesomelinus and Q. maurus, while in Q. m. kraussi the levels for pronotal and elytral characters are the highest of all specimens

measured although the rest of the characters are comparable.

6.4.2 Comparison of means and ranges for each character

From an analysis of means and ranges, species can be distinguished from one another using particular characters where the range falls outside that of another. However, where sample sizes are high means can be compared. The extent of the range for each character relates to the coefficient of variation as discussed previously. The more important characters are discussed.

a) Pronotum Length (Fig. 6.7)

The ranges of Q. mesomelinus and Q. maurus overlap considerably, while those of Q. maurus overlap and exceed slightly the lower half of the range of Q. mesomelinus. The mean values for the two species are, however, significantly different although those for Q. maurus do fall within the range of Q. mesomelinus.

Students 't' distribution values are as follows:-

British Q. mesomelinus and Q. maurus, $t = 5.601$, significant at $P = 0.05$ with 52 degrees of freedom (d.f.)

European Q. mesomelinus and Q. maurus, $t = 10.569$, significant at $P = 0.05$, 141 d.f.

British Q. maurus and European Q. maurus, $t = 0.121$, not significant at $P = 0.05$, 30 d.f.

British Q. mesomelinus and European Q. mesomelinus, $t = 1.683$, not significant at $P = 0.05$, 163 d.f.

British Q. mesomelinus and Extra-European Q. mesomelinus, $t = 1.139$, not significant at $P = 0.05$, 54 d.f.

The ranges of Q. m. kraussi and Q. skoraszewskyi encompass those of Q. mesomelinus and Q. maurus, however the mean for Q. m. kraussi falls between those of Q. mesomelinus and Q. maurus.

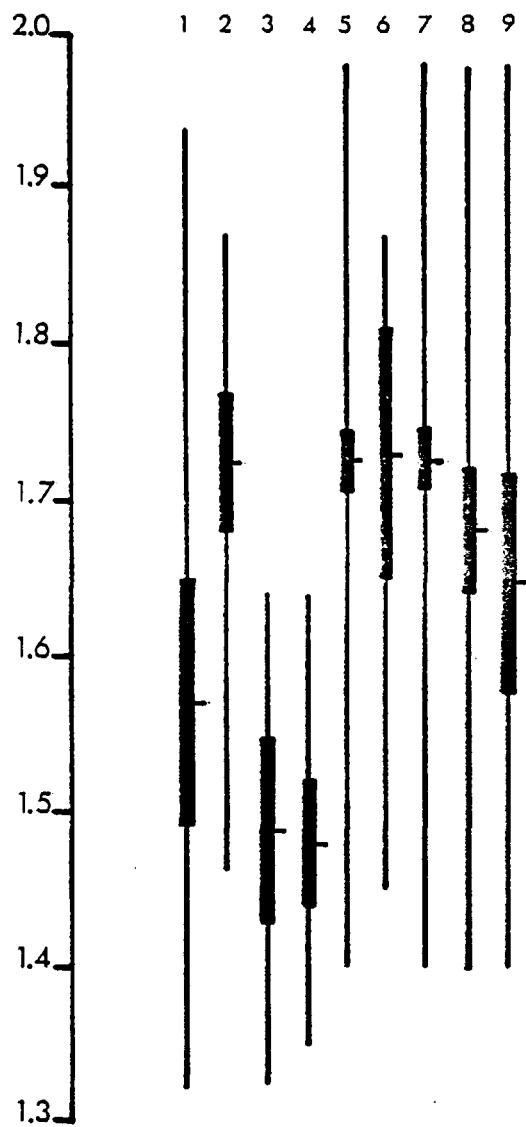
Although only two individuals of Q. m. fiorii were seen it might prove significant that they overlapped but exceeded the upper range of Q. mesomelinus.

Figs. 6.7 & 6.8. Comparison of means and ranges for pronotum length (6.7), and pronotum breadth (6.8) in Quedius species. 95% confidence limits indicated.

1. Q.m.kraussi
2. Q.skoraszewskyi
3. British Q.maurus
4. European Q.maurus
5. European Q.mesomelinus
6. Extra-european Q.mesomelinus
7. All Q.mesomelinus
8. British Q.mesomelinus
9. Pontrilas Q.mesomelinus

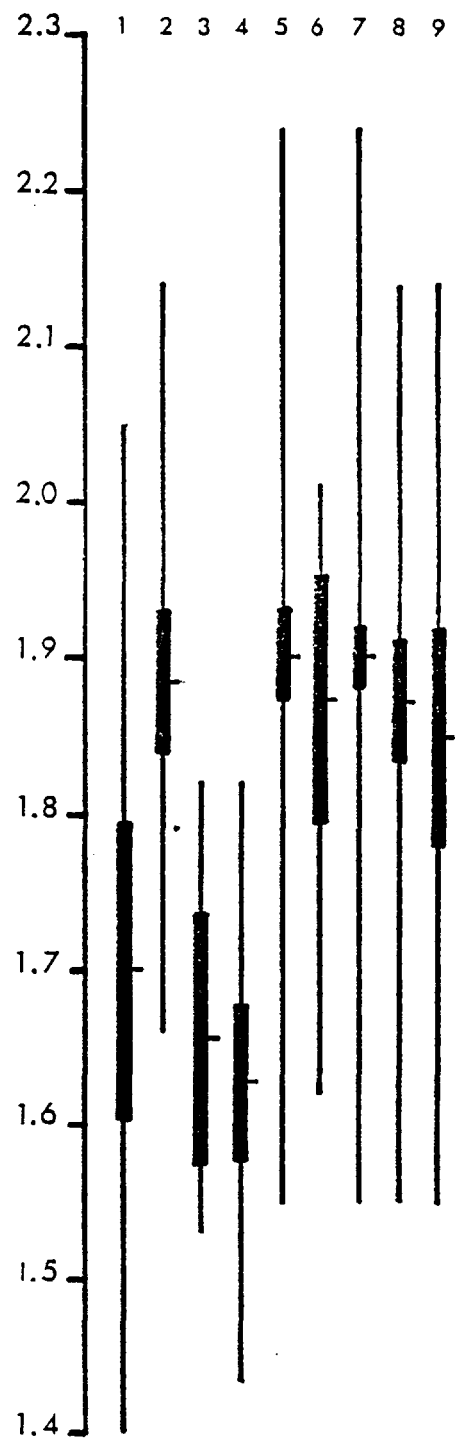
6.7

Pronotum Length



6.8

Pronotum Breadth



The mean values of British Q. mesomelinus are smaller than those of Continental European and Extra-European Q. mesomelinus which may be an indication of a cline in pronotum length. These values are, however, not significantly different using a Students 't' distribution.

b) Pronotum Breadth (Fig. 6.8)

This presents a similar picture to Pronotum length.

c) Elytral Length (Fig. 6.9)

While the ranges of Q. mesomelinus, Q. maurus, Q. m. kraussi and Q. skoraszewskyi overlap, the mean values offer some distinction between Q. mesomelinus, Q. maurus, and Q. m. kraussi.

d) Elytral Breadth (Fig. 6.10)

Ranges all fall within those for Q. mesomelinus, but means for Q. maurus are lower.

e) Median lobe Length (Fig. 6.11)

The ranges for all the species are narrower indicating increased constancy, however, they still overlap. It is interesting that the mean values of British Q. mesomelinus are so different from other Q. mesomelinus; this may be further evidence for a cline. Students 't' distribution values are as follows:-

British and European Q. mesomelinus, $t = 6.089$, significant at $P = 0.05$, 161 d.f.

British and Extra-European Q. mesomelinus, $t = 5.065$, significant at $P = 0.05$, 53 d.f.

The means for Q. maurus are distinct from Q. mesomelinus, and also that for Q. skoraszewskyi, the range exceeding the higher end of the Q. mesomelinus range.

Students 't' distribution values are as follows:-

British and European Q. maurus, $t = 0.03125$, not significant at $P = 0.05$, 28 d.f.

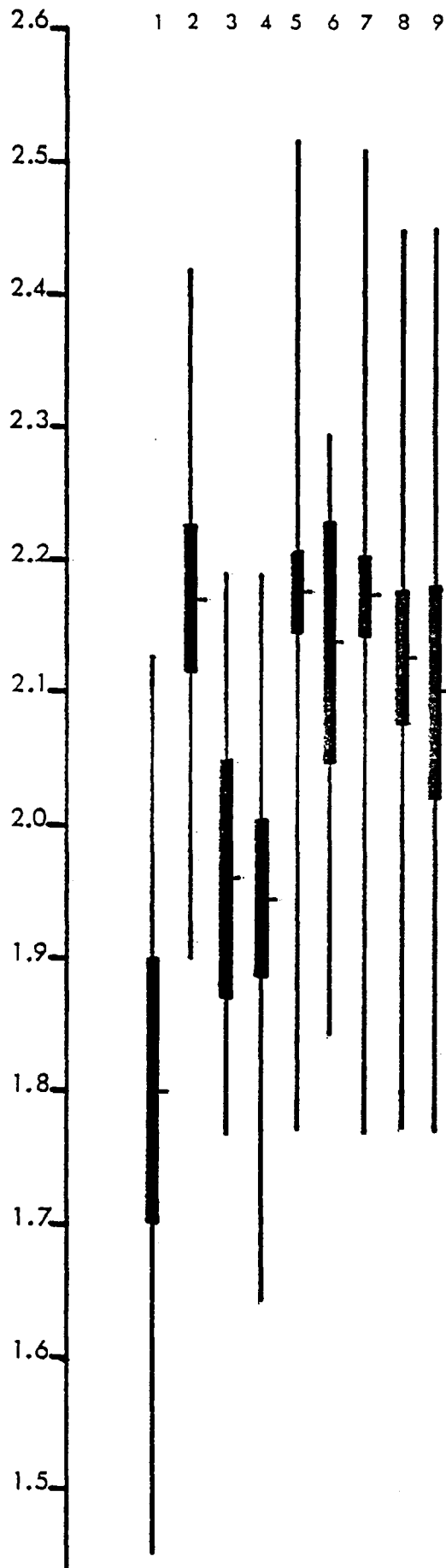
British Q. mesomelinus and Q. maurus, $t = 5.446$, significant at $P = 0.05$, 51 d.f.

Figs.6.9 & 6.10. Comparison of means and ranges for elytron length (6.9), and elytron breadth (6.10). 95% confidence limits indicated.

1. Q.m.kraussi
2. Q.skoraszewskyi
3. British Q.maurus
4. European Q.maurus
5. European Q.mesomelinus
6. Extra-european Q.mesomelinus
7. All Q.mesomelinus
8. British Q.mesomelinus
9. Pontrilas Q.mesomelinus

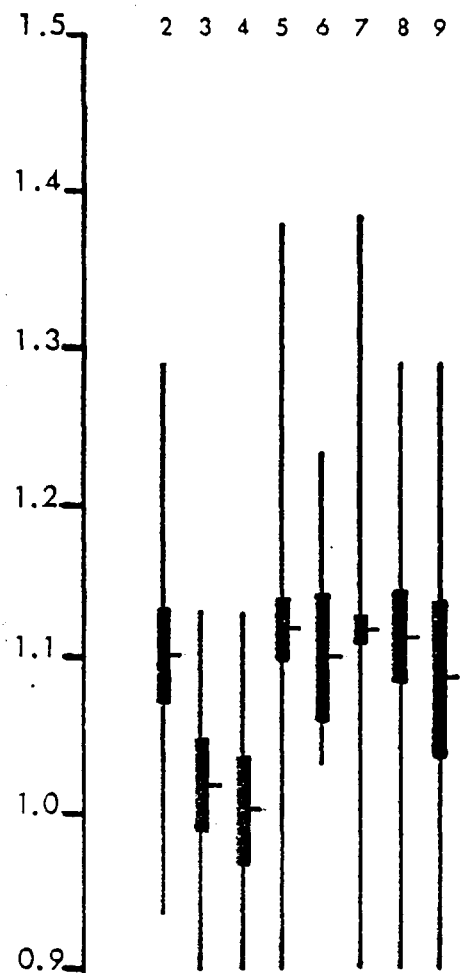
6.9

Elytron Length



6.10

Elytron Breadth

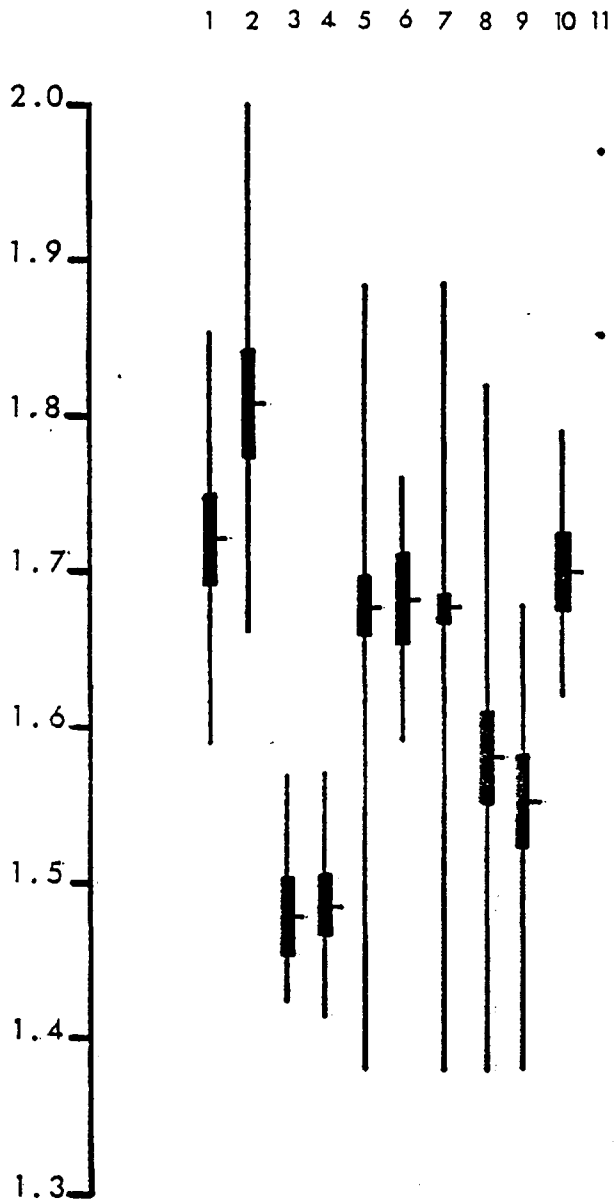


Figs.6.11 & 6.12. Comparison of means and ranges for median lobe length (6.11) and distance between < > (6.12). 95% confidence limits indicated.

1. Q.m.kraussi
2. Q.skoraszewskyi
3. British Q.maurus
4. European Q.maurus
5. European Q.mesomelinus
6. Extra-european Q.mesomelinus
7. All Q.mesomelinus
8. British Q.mesomelinus
9. Pontrilas Q.mesomelinus
10. Falkland Island Q.mesomelinus
11. Shetland Island Q.mesomelinus

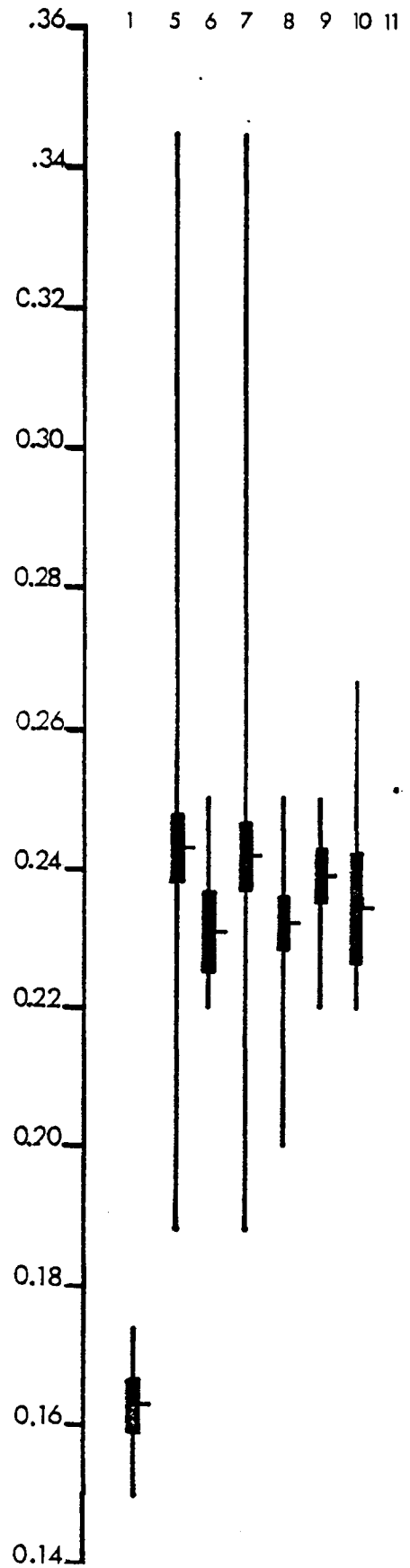
6.11

Median Lobe Length



6.12

Distance Between < >



European Q. mesomelinus and Q. maurus, $t = 13.86$, significant
at $P = 0.05$, 138 d.f.

All Q. mesomelinus and Q. skoraszewskyi, $t = 6.76$, significant
at $P = 0.05$, 159 d.f.

f) Distance between < > (Fig. 6.12)

The range and mean for Q. m. kraussi is distinct from
Q. mesomelinus ($t = 10.43$, significant at $P = 0.05$, 148 d.f.).
It is noteworthy that this character in Q. m. silensis is also
distinct, the apical projections are more widely spaced than in
Q. mesomelinus. This character is absent in Q. maurus and
Q. skoraszewskyi.

g) Apex strut length (Fig. 6.13)

Q. maurus, Q. skoraszewskyi and Q. m. kraussi have an overall
longer strut length than Q. mesomelinus.

h) Lateral lobe length (Fig. 6.14)

Only Q. skoraszewskyi exhibits any appreciable difference from
the other species in lateral lobe length. (All Q. mesomelinus and
Q. skoraszewskyi, $t = 9.52$, significant at $P = 0.05$, 160 d.f.).

The Shetland Island Q. mesomelinus may prove to be markedly
different in this character, since the three specimens measured fall
outside the range of other Q. mesomelinus.

i) Peg pattern length (Fig. 6.15)

Q. maurus is distinctly different. (All Q. mesomelinus and
European Q. maurus, $t = 26.22$, significant at $P = 0.05$, 153 d.f.)

j) Length/Breadth Pronotum and Length/Breadth Elytron, (Fig. 6.16,
& 6.17)

All the mean values for each species are not significantly
different as expected.

Students 't' distribution values are as follows:-

Length/Breadth Pronotum

All Q. mesomelinus and European Q. maurus, $t = 0.101$, not
significant at $P = 0.05$, 154 d.f.

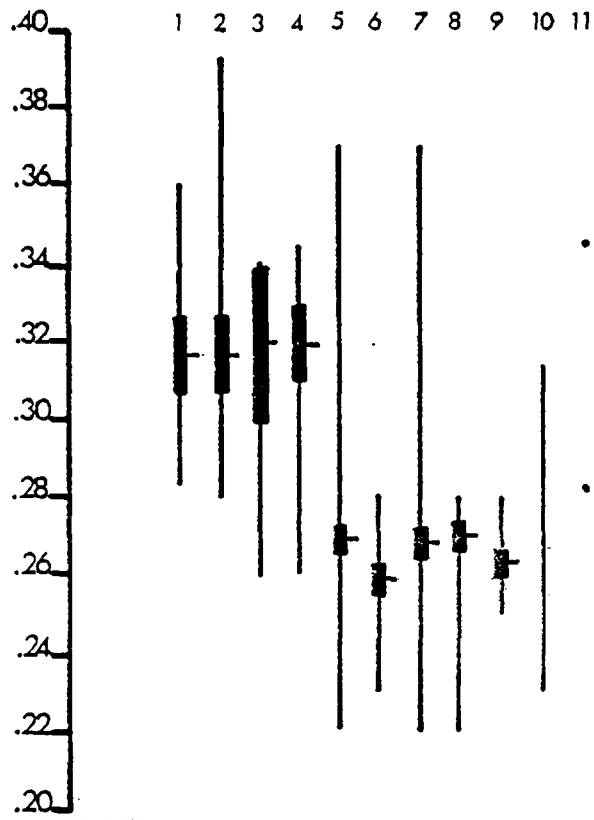
Figs. 6.13, 6.14, 6.15, & 6.16. Comparison of means and ranges for apex strut length (6.13), lateral lobe length (6.14), peg pattern length (6.15) and length/breadth pronotum (6.16).

1. Q.m.kraussi
2. Q.skoraszewskyi
3. British Q.maurus
4. European Q.maurus
5. European Q.mesomelinus
6. Extra-european Q.mesomelinus
7. All Q.mesomelinus
8. British Q.mesomelinus
9. Pontrilas Q.mesomelinus
10. Falkland Island Q.mesomelinus
11. Shetland Island Q.mesomelinus

95% confidence limits indicated.

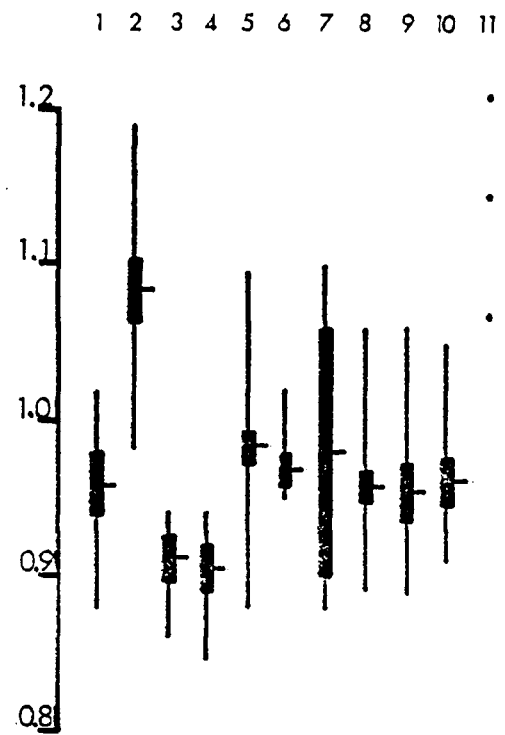
6.13

Apex Strut Length



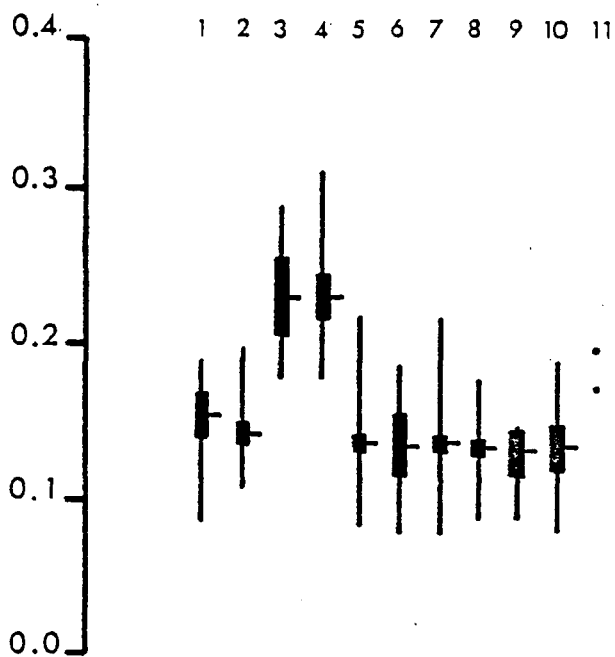
6.14

Lateral Lobe Length



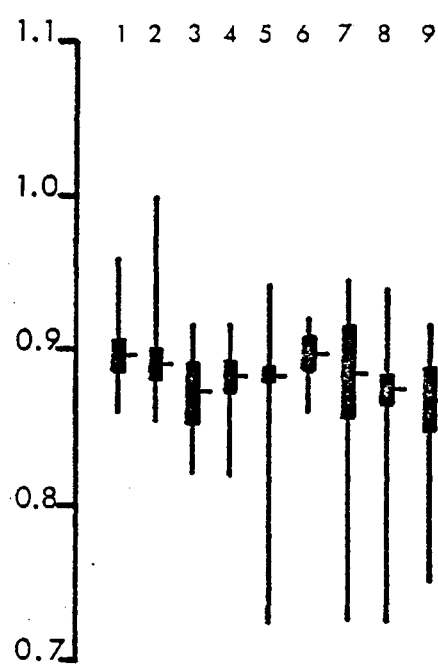
6.15

Peg Pattern Length



6.16

Length/Breadth Pronotum



All Q. mesomelinus and Q. skoraszewskyi, $t = 0.942$, not significant at $P = 0.05$, 162 d.f.

All Q. mesomelinus and Q. m. kraussi, $t = 1.752$, not significant at $P = 0.05$, 153 d.f.

Length/Breadth Elytra

All Q. mesomelinus and European Q. maurus, $t = 0.242$, not significant at $P = 0.05$, 155 d.f.

All Q. mesomelinus and Q. skoraszewskyi, $t = 0.283$, not significant at $P = 0.05$, 163 d.f.

The ranges for length/breadth pronotum are extremely narrow which makes this character particularly useful as a constant for all species against which other specifically different characters may be compared.

k) Pronotum length/Median lobe length (Fig. 6.18)

The differences in mean between Q. mesomelinus and the other species are significant. Students 't' distributions are as follows:-

All Q. mesomelinus and European Q. maurus, $t = 2.414$, significant at $P = 0.05$, 148 d.f.

All Q. mesomelinus and Q. skoraszewskyi, $t = 5.213$, significant at $P = 0.05$, 157 d.f.

All Q. mesomelinus and Q. kraussi, $t = 5.753$, significant at $P = 0.05$, 148 d.f.

l) Lateral lobe length/Peg pattern length (Fig. 6.19)

This enhances the differences in both characters between species, particularly between Q. maurus and Q. mesomelinus.

m) Median lobe length/lateral lobe length (Fig. 6.20)

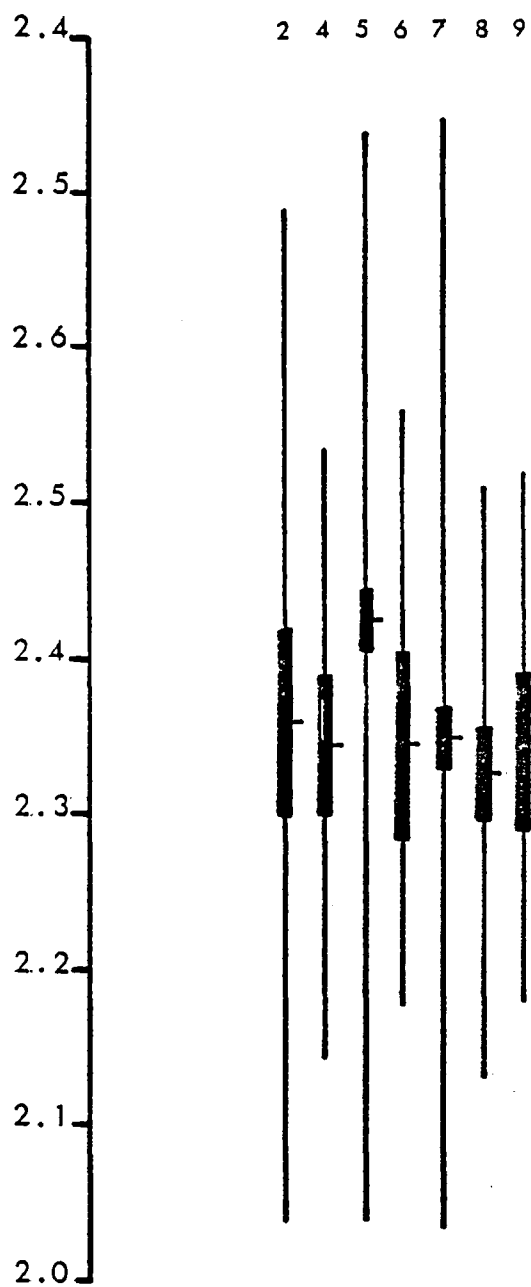
This further highlights the possibility of a cline across Europe from north to south. Mean values for British Q. mesomelinus are much less than those for Continental European individuals as a whole, whilst Yugoslavian Q. m. kraussi have a higher mean value and Italian Q. m. silensis a very much greater mean. Students 't' distribution values are as follows:-

Figs 6.17 & 6.18. Comparison of means and ranges for length/breadth
elytron (6.17) and pronotum length/ median lobe length
(6.18). 95% confidence limits indicated.

1. Q.m.kraussi
2. Q.skoraszewskyi
3. British Q.maurus
4. European Q.maurus
5. European Q.mesomelinus
6. Extra-european Q.mesomelinus
7. All Q.mesomelinus
8. British Q.mesomelinus
9. Pontrilas Q.mesomelinus

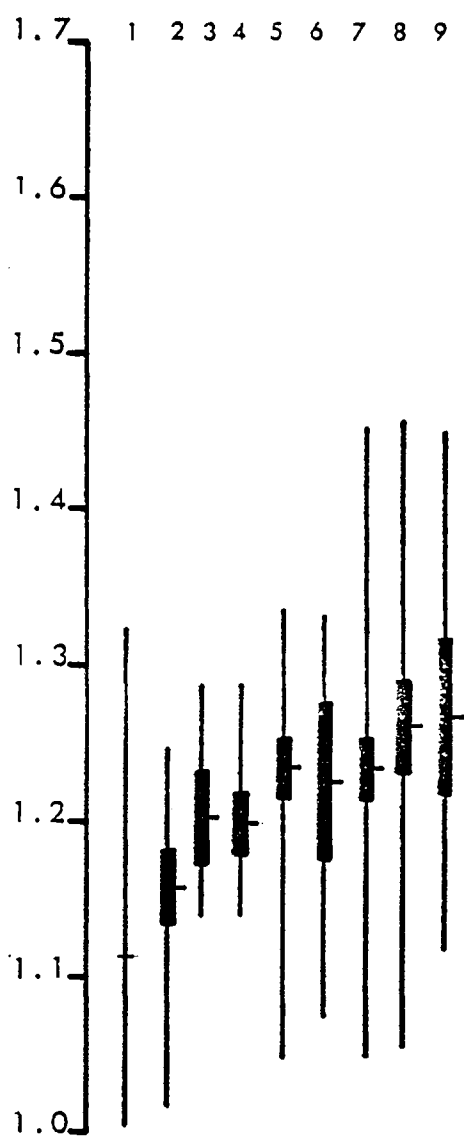
6.17

Length/Breadth Elytron



6.18

Pronotum Length/M.Lobe Length

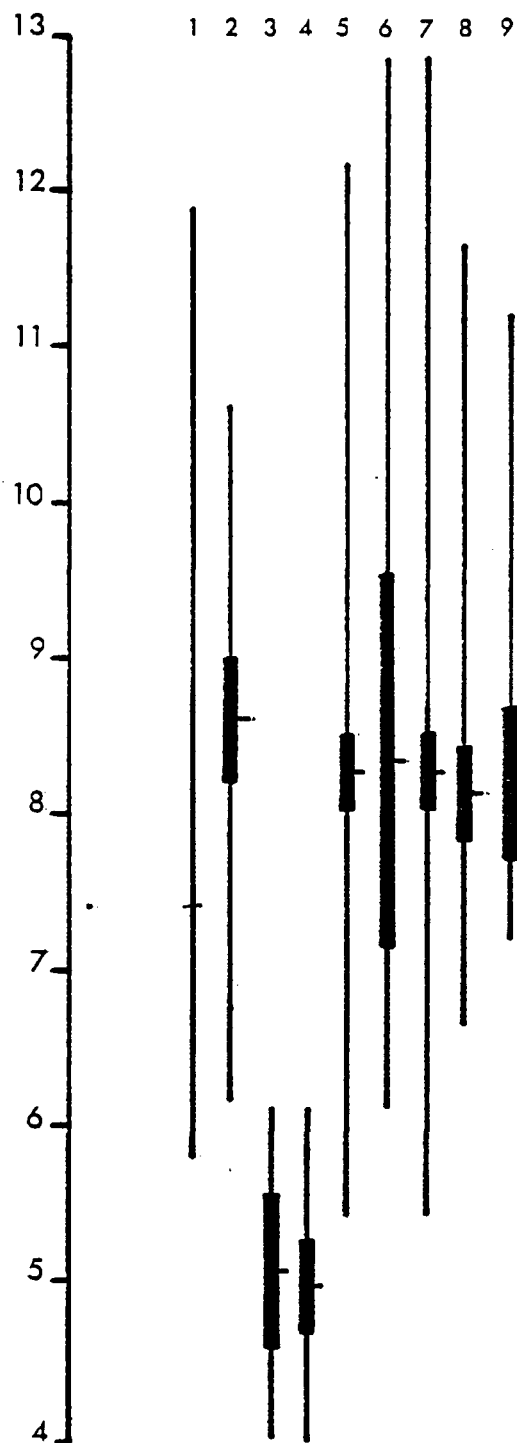


Figs.6.19 & 6.20. Comparison of means and ranges for lateral lobe length/
peg pattern length (6.19) and median lobe length/lateral
lobe length (6.20). 95% confidence limits indicated.

1. Q.m.kraussi
2. Q.skoraszewskyi
3. British Q.maurus
4. European Q.maurus
5. European Q.mesomelinus
6. Extra-european Q.mesomelinus
7. All Q.mesomelinus
8. British Q.mesomelinus
9. Pontrilas Q.mesomelinus

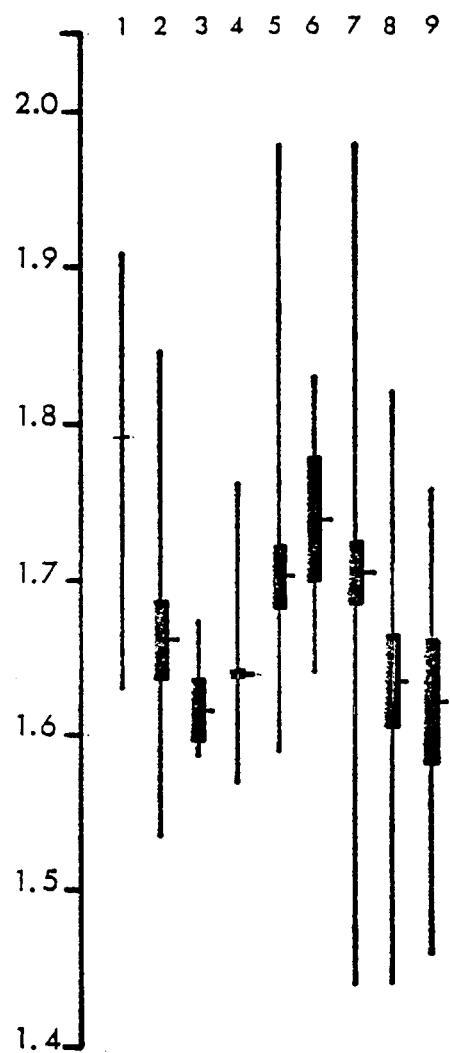
6.19

L.Lobe Length / Peg Pattern Length



6.20

M.Lobe Length / L.Lobe Length



British and European Q. mesomelinus, $t = 3.938$, significant at $P = 0.05$, 159 d.f.

European Q. mesomelinus and Q. m. kraussi, $t = 4.694$ significant at $P = 0.05$, 138 d.f.

Although in most cases the ranges of variation overlap between species, which is to be expected in "varieties" of this type, some distinction is achieved by the use of sample means.

6.4.3 Comparison of species using bivariate plots

a) Length/breadth pronotum/length median lobe (Figs. 6.21-6.23)

Length/breadth pronotum is used here as a constant as previously discussed.

It is clear that Q. mesomelinus and Q. maurus are distinct with little overlap between the two, Q. maurus having a shorter median lobe. Q. maurus does, however, overlap with Q. mesomelinus from Britain at the shorter end of the range.

Q. mesomelinus from the single locality, near Pontrilas, reflects the amount of variation in all British Q. mesomelinus. There is, however, a very noticeable trend in length of median lobe, Continental European individuals have distinctly longer median lobes compared with those from British locations. This is analysed on a geographical basis in a later section.

Individuals of Q. mesomelinus from outside Britain and Europe possess median lobe lengths which are intermediate between Continental European and British populations. Q. mesomelinus populations outside Europe are not part of the endemic fauna. It would be valuable to ascertain their origins and then examine their structural stability in an isolated environment, where there are no closely related sympatric species, compared to populations in Europe.

In general Q. skoraszewskyi individuals have longer median lobes than Continental European Q. mesomelinus, but there is a considerable overlap between them from about the centre of their ranges. It is

Fig.6.21. Graph comparing length/breadth pronotum / median lobe length in British and European Quedius mesomelinus.

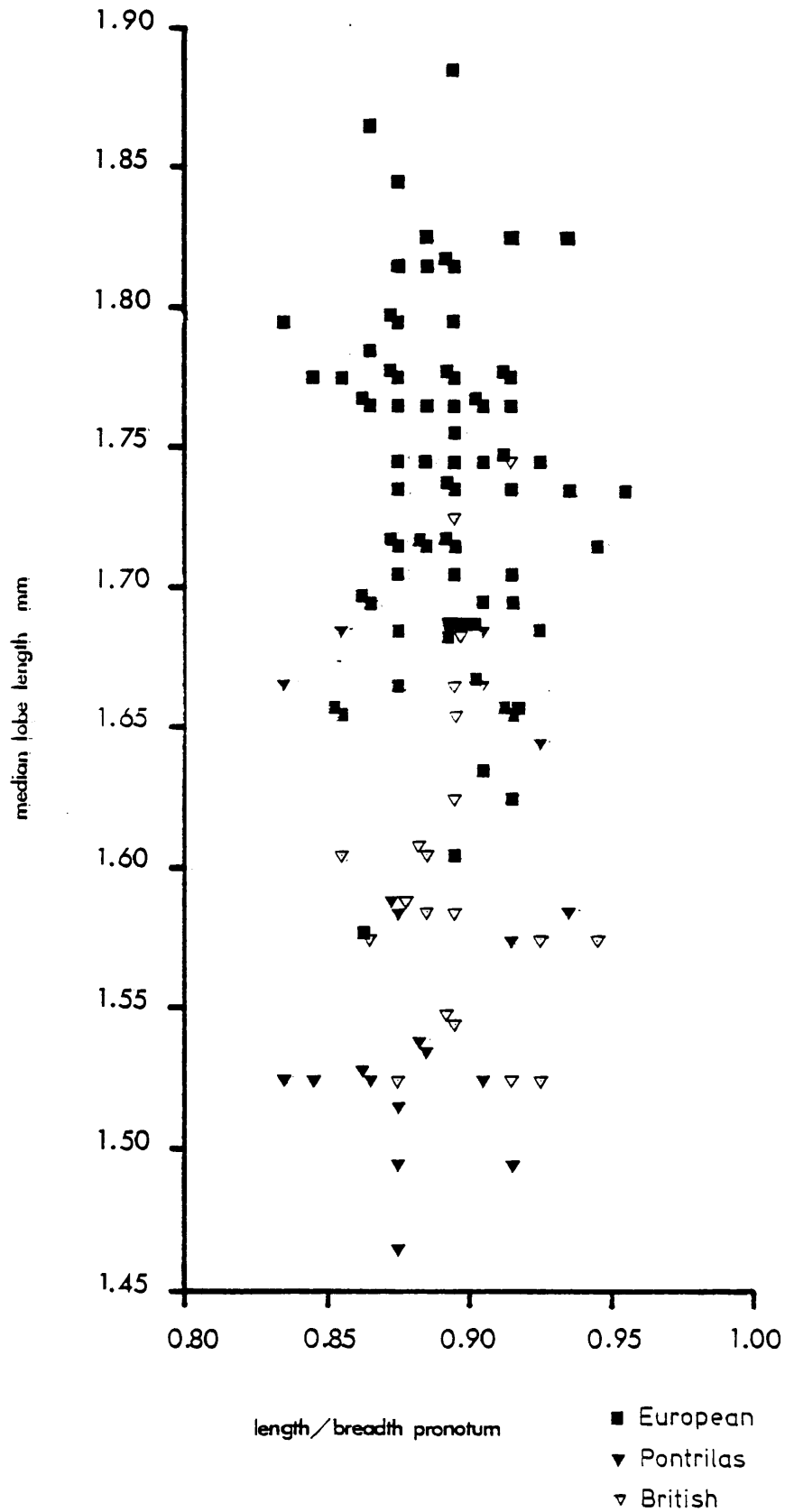


Fig.6.22. Graph comparing length/breadth pronotum / median lobe length
in European Quedius mesomelinus, Q.m.kraussi and Q.maurus.

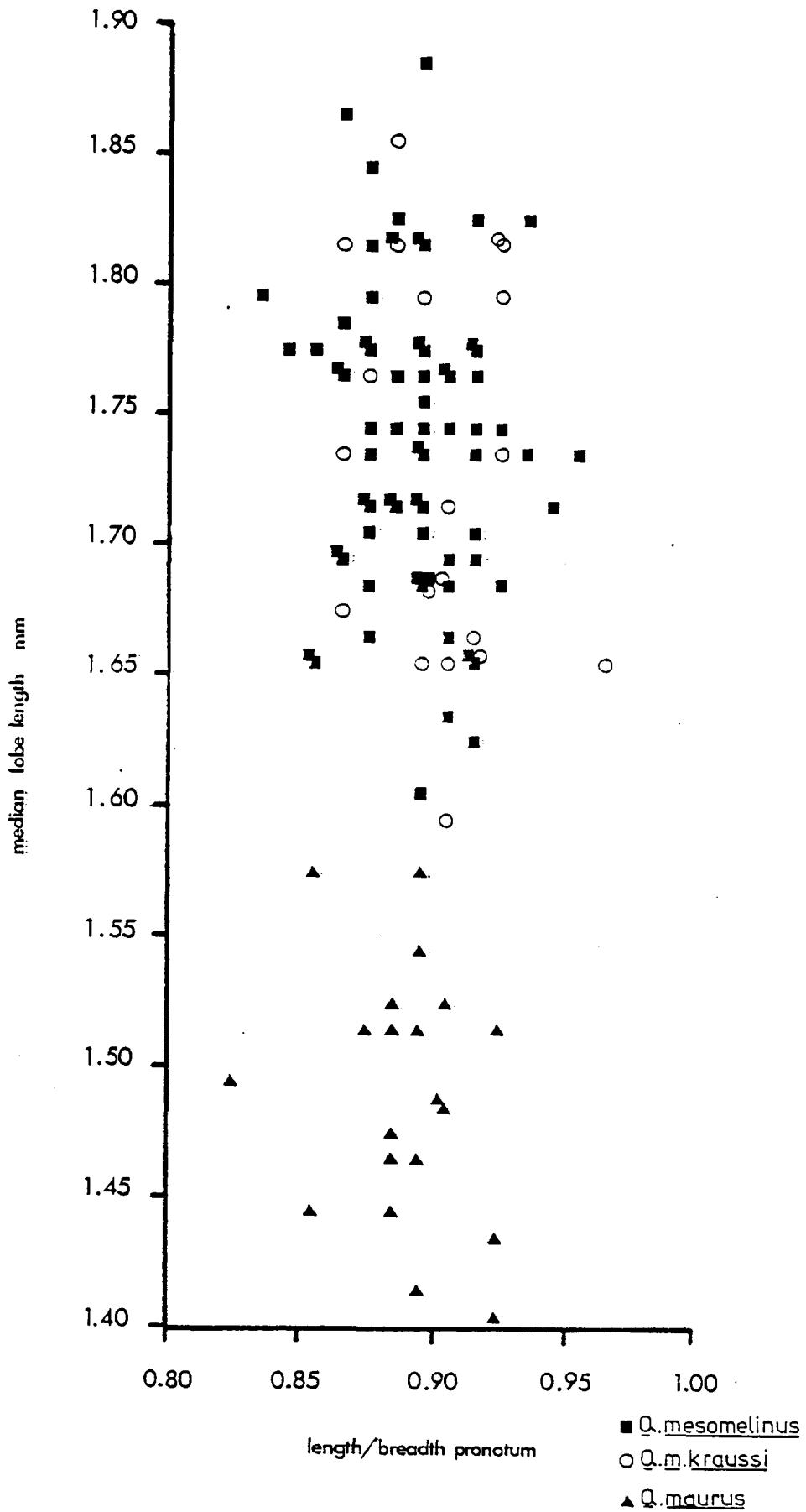
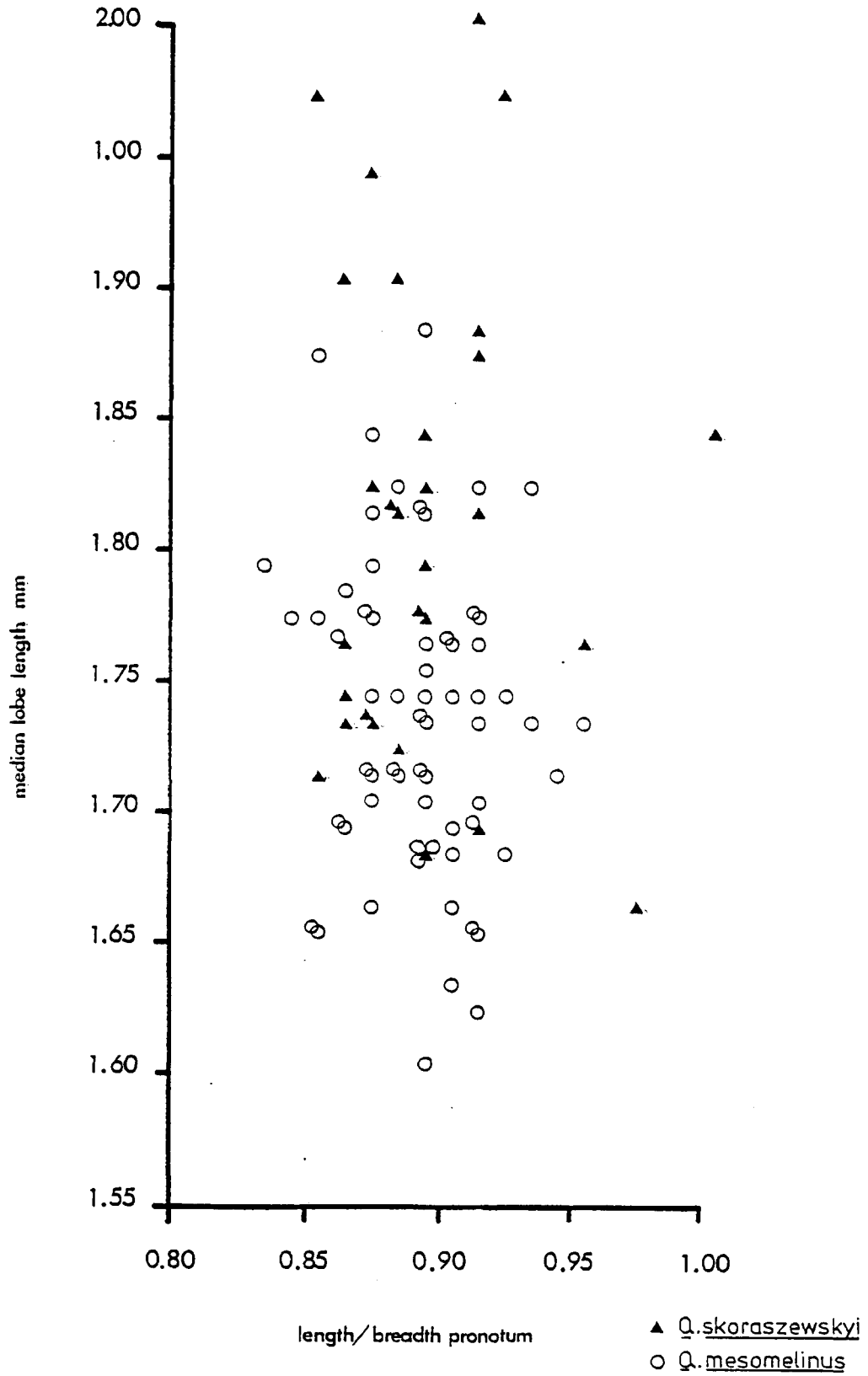


Fig.6.23. Graph comparing length/breadth pronotum / median lobe length in European Q.mesomelinus and Q.skoraszewskyi.



necessary to discover whether populations of Q. skoraszewskyi and Q. mesomelinus truly overlap geographically or whether, as seems most likely, Q. skoraszewskyi is adapted to colder conditions, being found at high altitudes in the Alps, and is thereby completely isolated from Q. mesomelinus. Unfortunately there is not sufficient data to unravel this dilemma.

The range of Q. m. kraussi completely overlaps that of Continental European Q. mesomelinus.

b) Median lobe length/lateral lobe length (Figs. 6.24-6.26)

A combination of median lobe length and lateral lobe length provides a better separation to distinguish the species more clearly.

Q. maurus is distinct but with a small overlap with British Q. mesomelinus. Q. maurus has a short median and lateral lobe and there is virtually no overlap with Continental European Q. mesomelinus. The median lobe size increase in Continental European Q. mesomelinus is again obvious; but there is no similar trend for the lateral lobe which remains more or less within the same limits all over Britain and Continental Europe. The Falkland Island individuals of Q. mesomelinus fall in the centre of the range of the Continental European individuals, only overlapping at the extreme end of the British Q. mesomelinus range. Individuals of Q. skoraszewskyi are fairly distinct from Continental European Q. mesomelinus owing to the longer length of both median and lateral lobes.

Q. m. kraussi again overlap with Continental European Q. mesomelinus but is quite distinct from Q. skoraszewskyi, owing to a shorter lateral lobe.

c) Lateral lobe length/peg pattern length (Figs. 6.27-6.29)

A combination of lateral lobe length and peg pattern length provides the best separation of Q. maurus from Q. mesomelinus owing to the shorter lateral lobe and, particularly, the long peg pattern.

Fig.6.24. Graph comparing lateral lobe length / median lobe length in British and European Quedius mesomelinus.

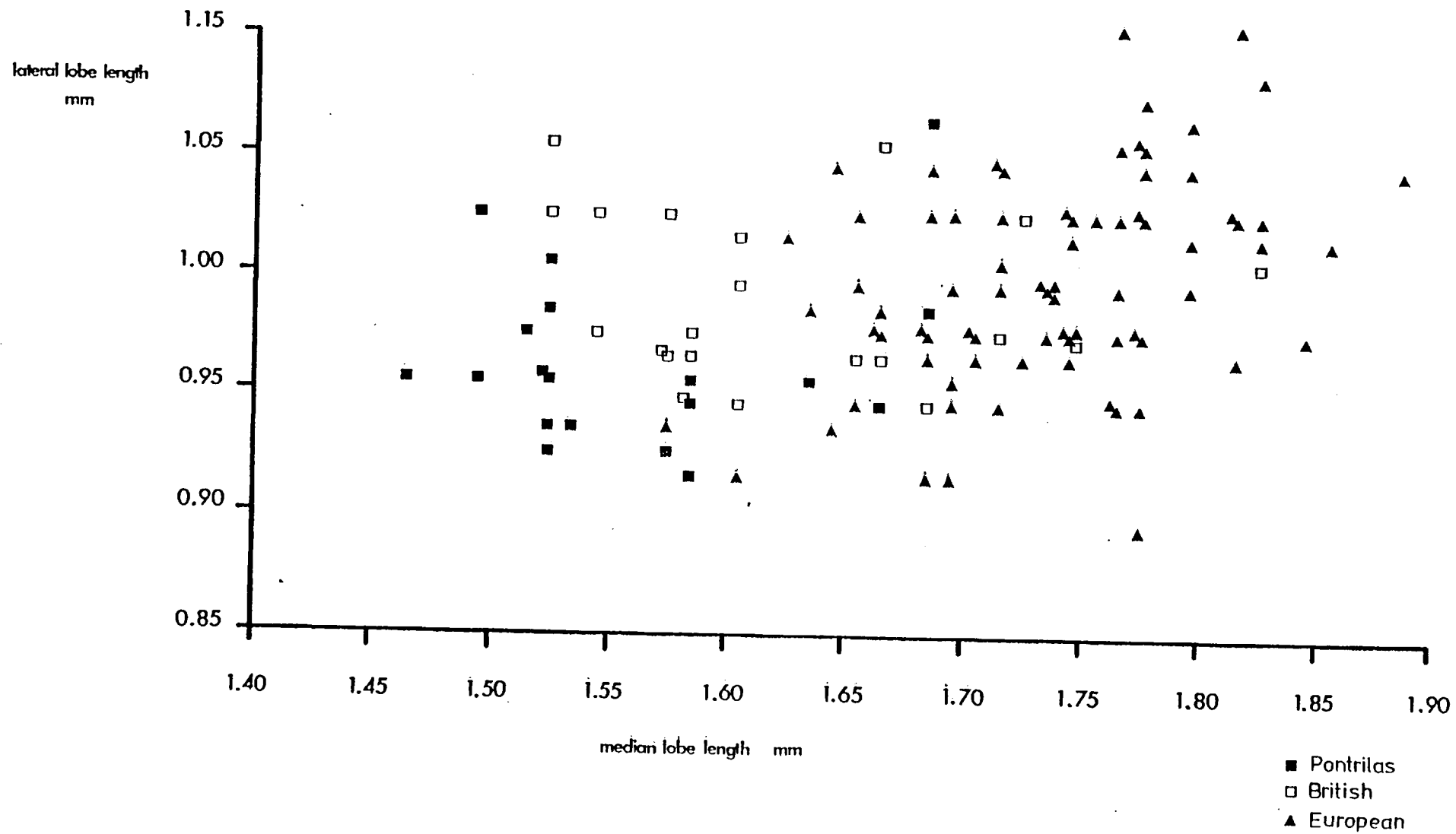


Fig. 6.25. Graph comparing lateral lobe length / median lobe length in European Quedius mesomelinus, Q. skoraszewskyi, Q. m. kraussi and Q. maurus.

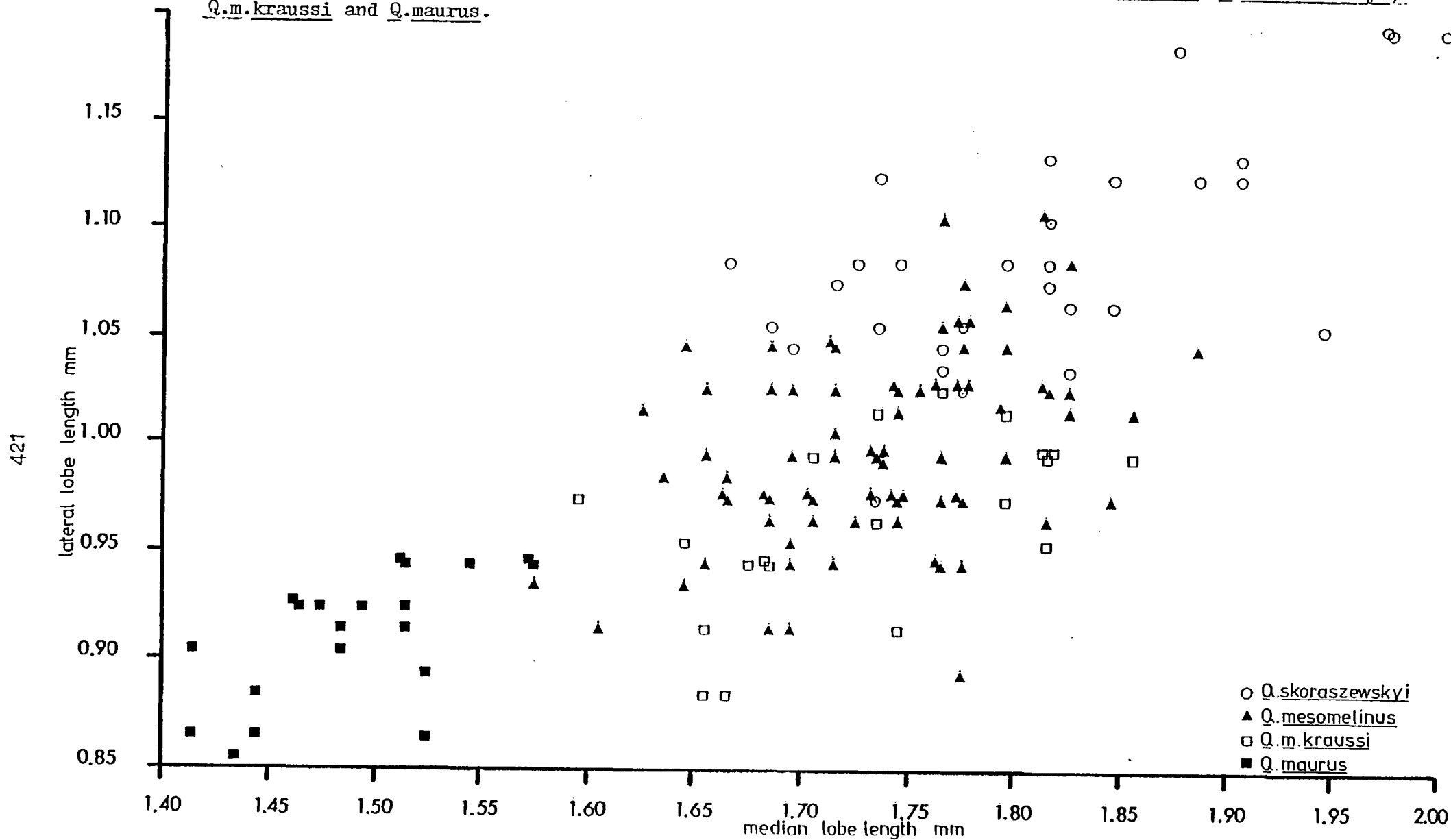


Fig.6.26. Graph comparing lateral lobe length / median lobe length in European Quedius mesomelinus and Falkland Island Q.mesomelinus.

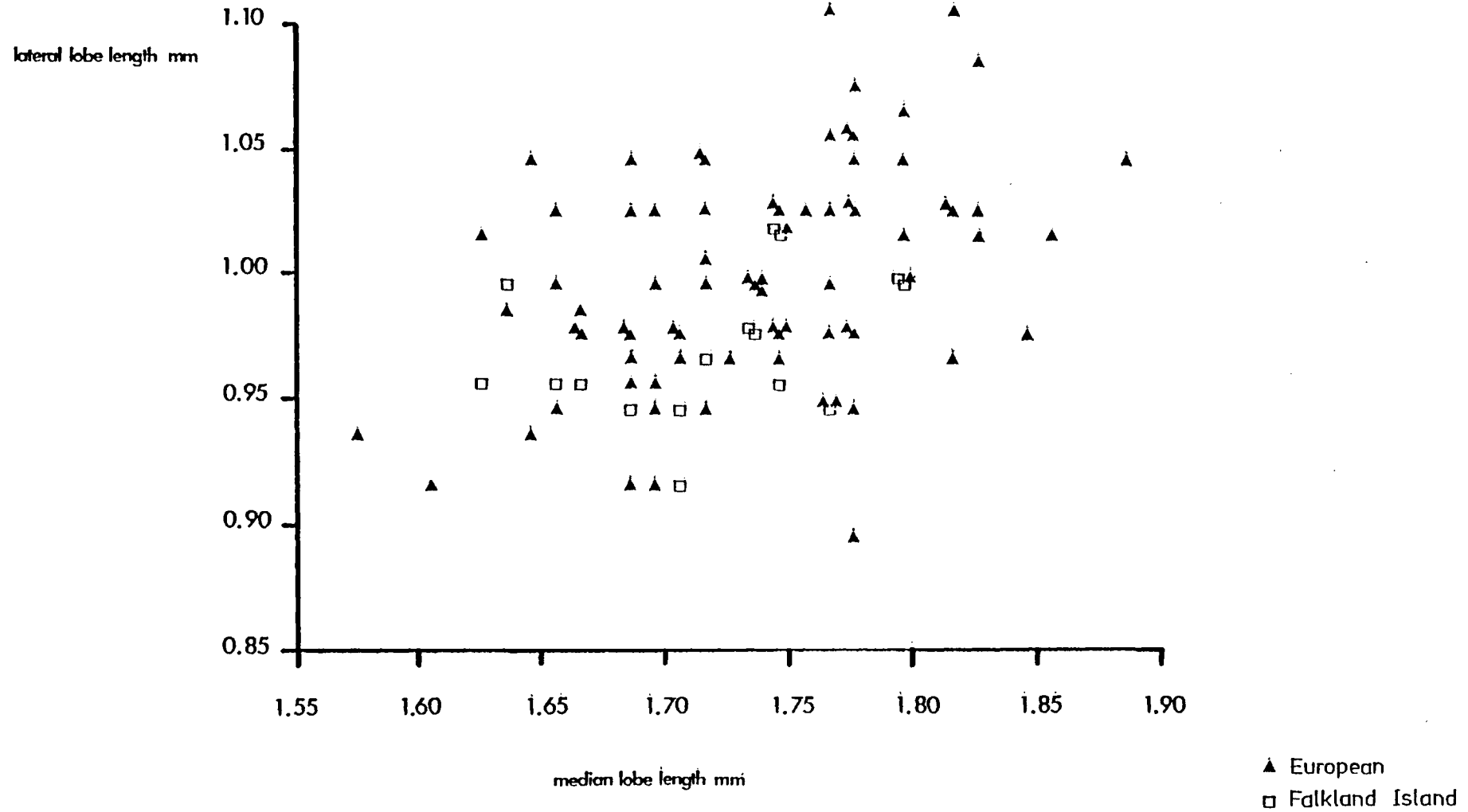


Fig.6.27. Graph comparing peg pattern length / lateral lobe length in European Quedius mesomelinus, Q.maurus and Q.skoraszewskyi.

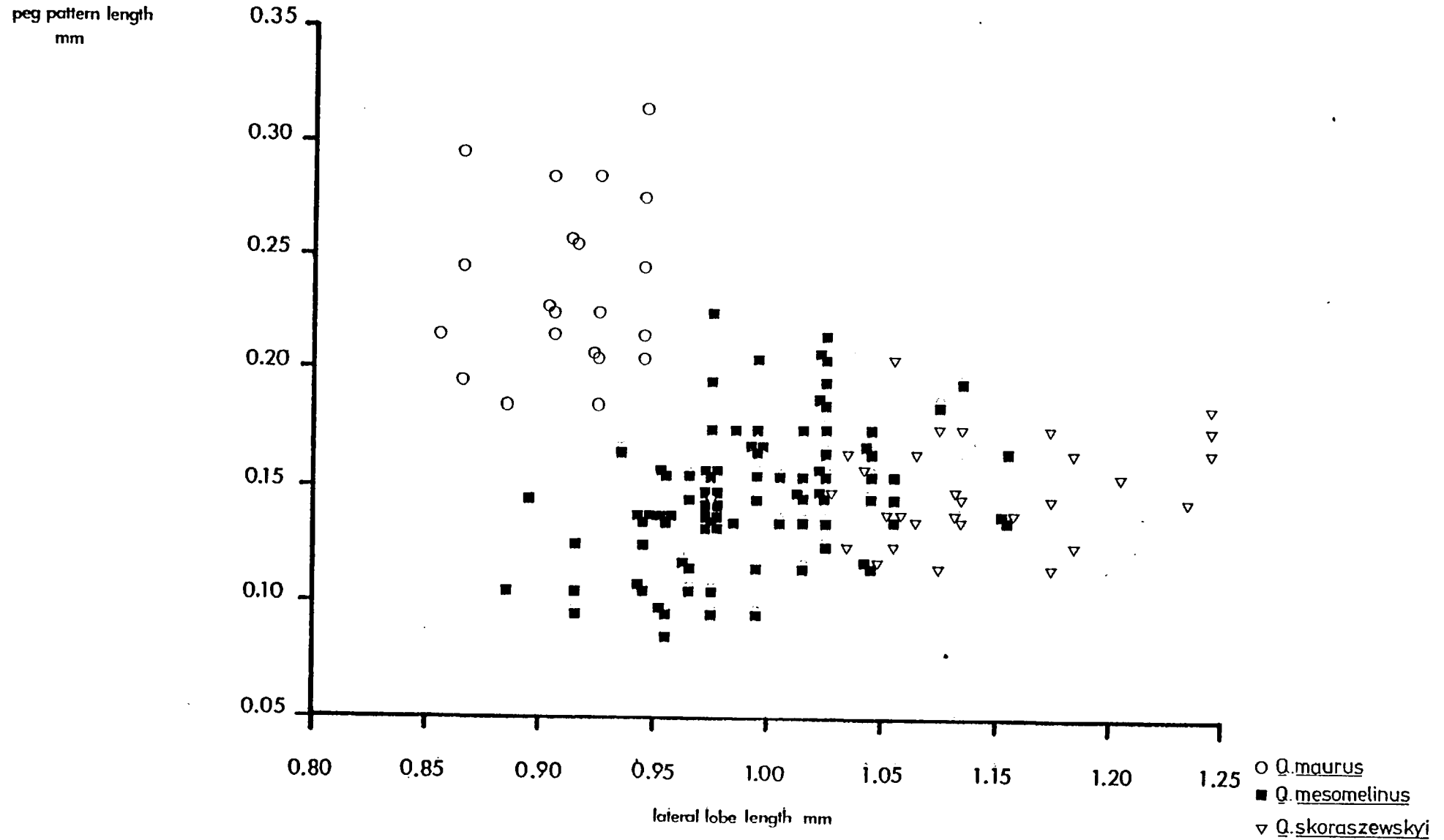


Fig.6.28. Graph comparing peg pattern length / lateral lobe length in European Quedius mesomelinus and Q.m.kraussi.

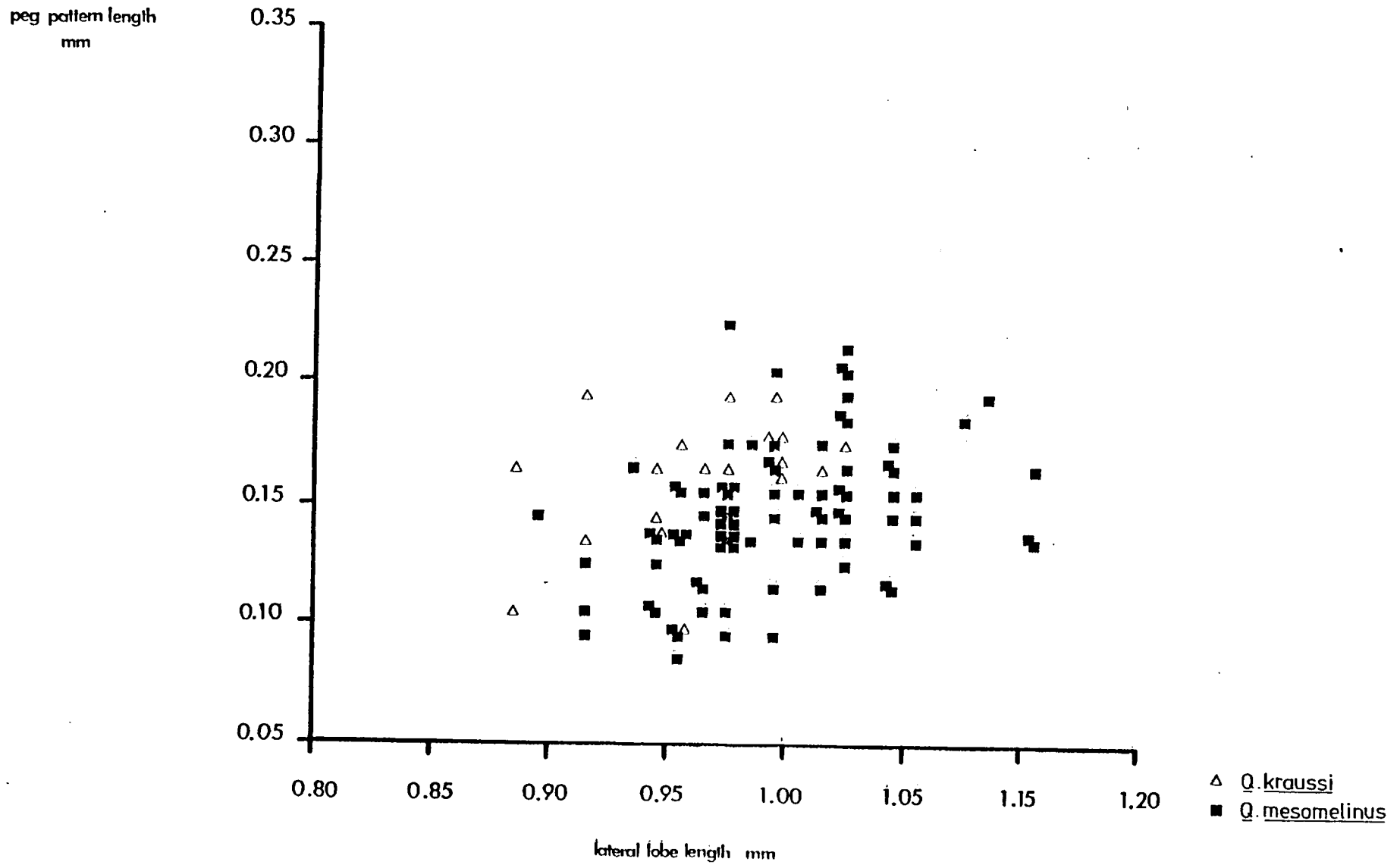
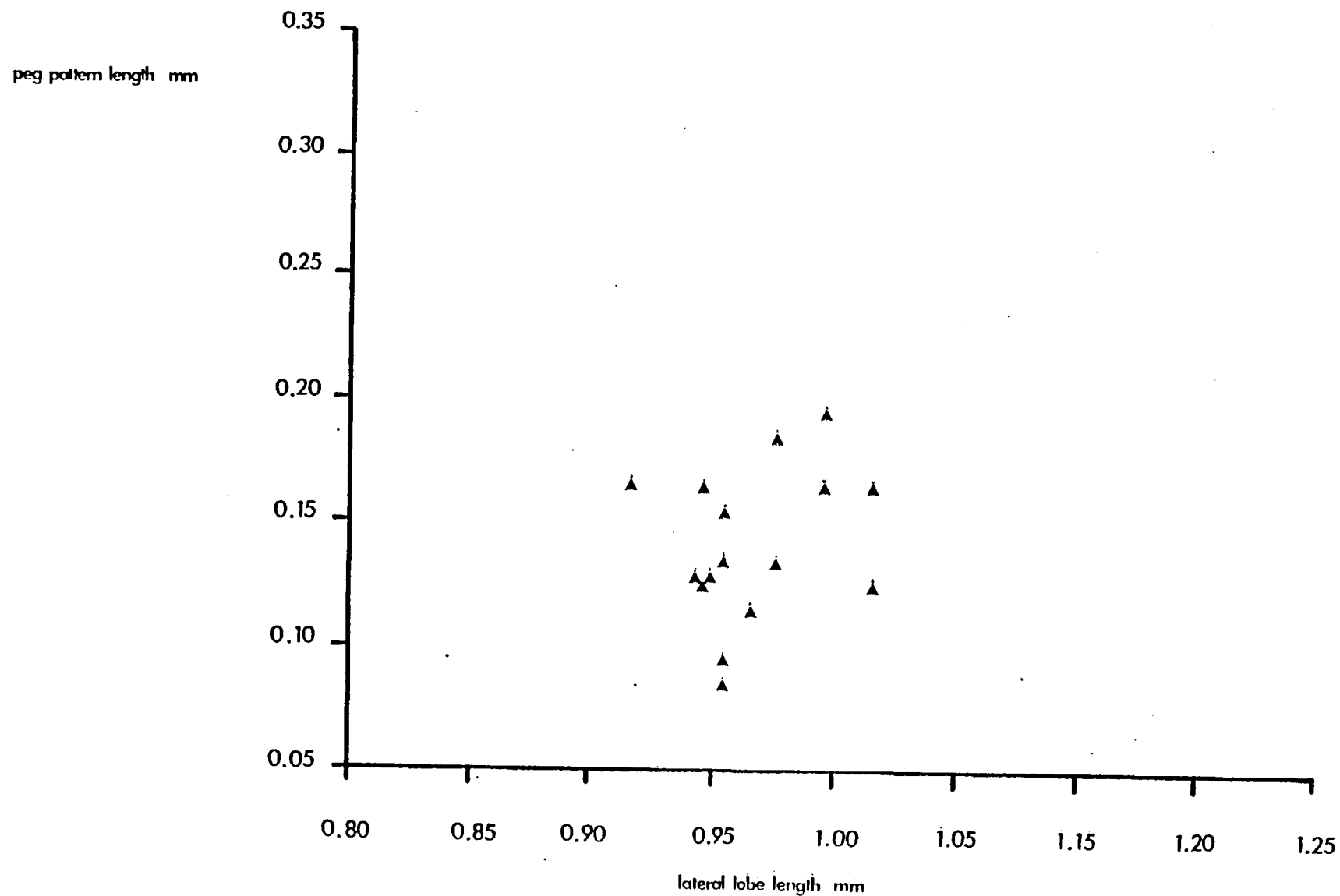


Fig.6.29. Graph showing peg pattern length / lateral lobe length in Falkland Island Quedius mesomelinus.



Likewise this combination separates Q. skoraszewskyi from other Q. mesomelinus and very distinctly from Q. m. kraussi, but this is only on the basis of the longer lateral lobe.

Peg pattern length is, however, not a good character for separating geographical populations of Q. mesomelinus. British, Continental European, and Falkland Island Q. mesomelinus all overlap within a reasonably tight range, which emphasises the stability in these characters with varying geographical location and is probably, therefore, an indication of their importance in specific mate recognition.

Q. m. kraussi, while overlapping with Q. mesomelinus, falls in a position between Q. maurus and Q. mesomelinus. However, further specimens would be needed to confirm this.

6.4.4 Geographical trend in median lobe length

It has already been noted that the difference in mean lengths of the median lobe apparent between British and Continental European Q. mesomelinus may be an indication of a geographical cline.

If Europe is divided into arbitrary sections, (Fig. 6.31) it can be shown that there is a distinct trend of increasing median lobe length in a north-west to south-east direction across Europe (Fig. 6.30).

If an arbitrary length, say 1.7mm, is taken then the percentage of individuals reaching or exceeding that length in each sector is central and northern Britain 0%, southern Britain 27.27%, northern Europe 61.53% and southern Europe 69.64%.

The significance of the difference between means of the samples is tested using the Students 't' distribution.

C. & N. Britain and S. Britain, $t = 2.9508$ highly significant
at $P = 0.01$, 40 d.f.

S. Britain and N. Continental Europe, $t = 2.209$ significant
at $P = 0.05$, 22 d.f.

N. Continental Europe and S. Continental Europe, $t = 1.021$,
not significant at $P = 0.05$, 67 d.f. but
significant at $P = 0.20$.

Fig.6.30. Graph to show geographical trend in median lobe length of Quedius mesomelinus across Europe.

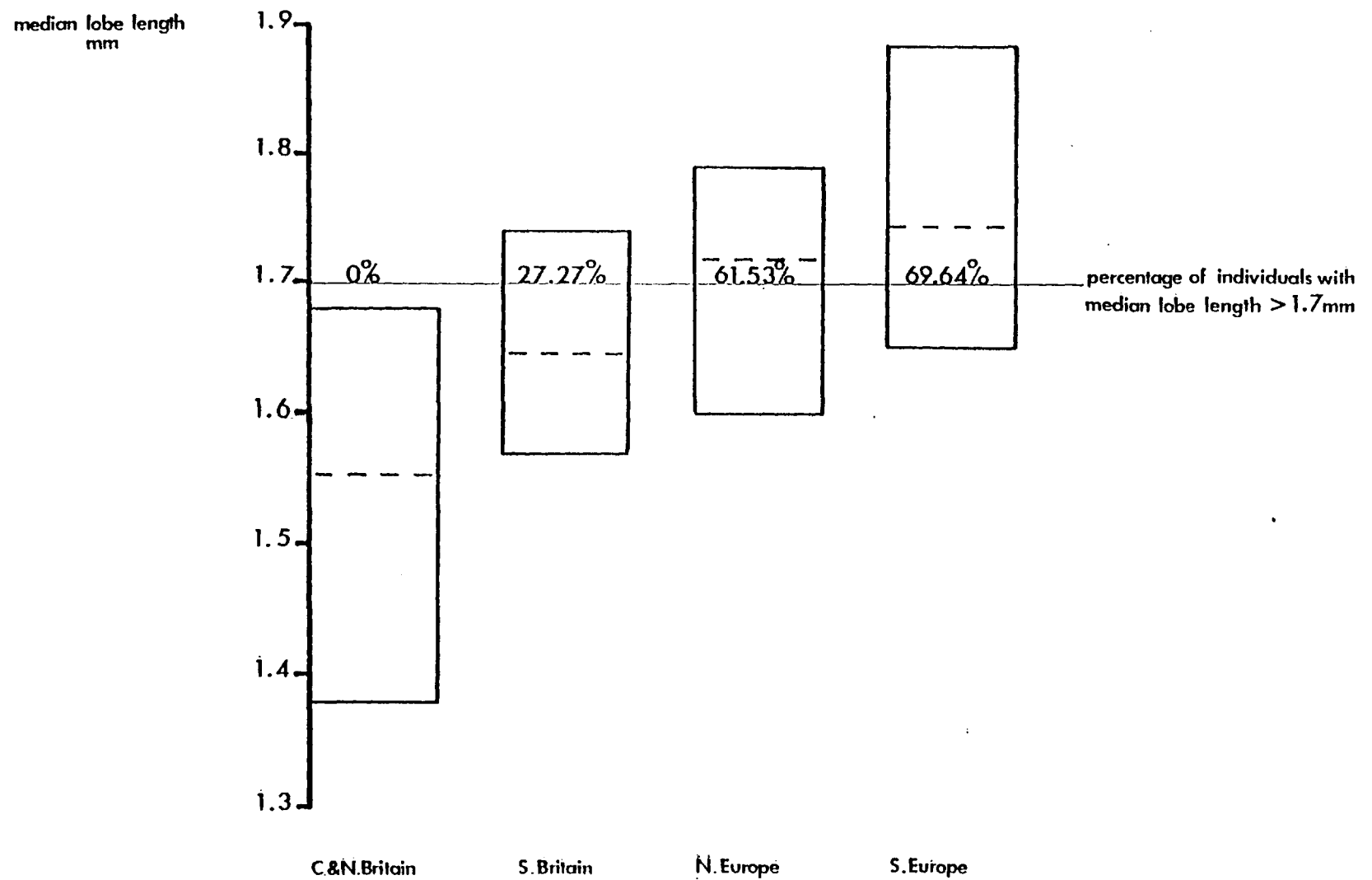


Fig.6.31 Map to show the division of Europe into arbitrary sections,

- a - central and northern Britain
- b - southern Britain
- c - northern Europe
- d - southern Europe



These show that while the median lobe length does increase in this manner, the cline gradually lessens in a south-easterly direction, the greatest differences being between Britain and the rest of Europe.

6.4.5 Correlation between median lobe length and pronotum length

Pronotum length can generally be used as an indicator of overall body size, since body length cannot be accurately measured because of the retractability of the abdomen in the Staphylinidae. Changes in pronotum length may therefore be related to size variation in other body characters, including perhaps the length of the genitalia. As with median lobe length it is apparent that in British and Continental European individuals there is an increase in pronotum length and breadth in more southerly individuals. If a factor such as temperature or climate were responsible for a geographical cline then median lobe length may be related to overall size, smaller insects occurring in lower temperatures.

The correlation coefficient between pronotum length and median lobe length is only 39.73% which is extremely low, indicating that although there is a very small increase in pronotum length across Europe it cannot be related to the increase in median lobe length. Therefore the change in median lobe length across Europe cannot be accounted for by an equivalent change in body size and some other factor acting on the median lobe alone is responsible for the cline.

6.5 Falkland Island *Q. mesomelinus*

Individuals from the Falkland Islands were studied in order to gain information on a relatively isolated population which is not part of the endemic fauna.

In comparison to other *Q. mesomelinus* populations, that in the Falkland Islands exhibits less variation in the median lobe length, lateral lobe length, distance from lateral lobe base to beginning of

peg pattern and in number of pegs.

The length of the peg pattern is more variable than in British and Continental European individuals and comparable with extra-European Q. mesomelinus.

The remaining characters (distance between median lobe apical projections, length of median lobe apical strut and breadth of median lobe apex) exhibit greater variation than in British individuals, but are either similar or less variable than those of Continental European individuals.

With regard to the ranges and means of genital characters compared with other Q. mesomelinus populations, the apex strut length, length of lateral lobe, distance from base of lateral lobe to start of peg pattern, distance $< >$, and peg pattern length overlap and are very similar to other populations of the species.

The mean length of the median lobe is very much greater than that of British and Continental European populations and more comparable to, but still greater than, extra-European individuals.

Student 't' distributions are as follows:-

Falkland Island and British Q. mesomelinus, $t = 6.619$, significant
at $P = 0.05$, 57 d.f.

Falkland Island and European Q. mesomelinus, $t = 1.395$, not significant
at $P = 0.05$, 134 d.f.

Falkland Island and Extra-European Q. mesomelinus, $t = 0.878$, not
significant at $P = 0.05$, 26 d.f.

The overall range is narrow but falls within those of the other Q. mesomelinus populations.

6.6 Shetland Island Q. mesomelinus

Only three individuals were examined, however, there are indications that they may be part of a diverging isolated population which is distinct from other British individuals in a number of characters.

The median lobe is longer than in all British individuals and exceeds the range of Continental European individuals. The median lobe apex strut length is larger than in all British individuals but falls within the range of Continental European individuals. The median lobe apical projections are very pronounced.

Similarly the lateral lobe length is longer than most other Q. mesomelinus individuals, but just overlaps with the upper range of Continental European Q. mesomelinus.

Further examinations are required before firm conclusions can be made.

6.7 Peg Patterns

The peg pattern, coupled with characters of the lateral lobe, is an important taxonomic character, but it is suggested that it also plays a role in specific mate recognition (Sections 3 and 4).

There are many cases where peg patterns are markedly different in closely related sympatric species, e.g. Philonthus , but comparable in allopatric species. This suggests that such a degree of difference may be necessary for specific distinction.

The "varieties" of Q. mesomelinus vary in their degree of difference from each other and this could be due to a number of reasons:

- they are separate species but are not sympatric.
- they are geographically isolated populations which are diverging and in the process of speciation.
- they are separate species and sympatric, but the degree of difference detected by the ♀ may be based on different criteria which are more subtle than can be detected in a subjective analysis.

The criteria which make up a peg pattern should be discussed in order to understand the differences and determine what is important

to the female in the process of recognition.

These include:

1. peg number
2. peg density
3. peg pattern length
4. peg pattern breadth
5. peg pattern position
 - a) distance from lateral lobe apex
 - b) distance from lateral lobe lateral margins
 - c) distance between peg groups.

The variation found in peg number and peg pattern length has already been discussed, emphasising that it is not the precise number and position of individual pegs which are important. The left and right groups of pegs on the lateral lobe are never identical and it is the position and shape of the overall pattern which remains constant for any particular species.

Q. maurus (Fig.6.4a-c)

Q. maurus is the most distinct species, the lateral lobe is of specific shape and the peg pattern consists of two irregular and closely aligned columns of peg setae which are situated away from the lateral margins of the lateral lobe. There are on average of 9.1 (left) : 8.6 (right) peg-setae in each column, extending over a mean distance of 0.231 mm. The mid-point of the column of pegs falls at approximately the widest point of the lateral lobe.

A value for peg density per unit length is given by $\frac{\text{peg pattern length}}{\bar{x} \text{ peg number}}$

and provides a sample mean value for Continental European Q. maurus of 0.025, which when compared with that for Continental European Q. mesomelinus of 0.0145 is significant ($t = 8.54$, $P = 0.05$, 44 d.f.).

Q. mesomelinus (Fig. 6.2)

The peg pattern consists of two elongate groups of pegs one on each side of the lateral lobe, near to the lateral edge at the widest

point. There are on average 10.55 (left) : 10.50 (right) peg setae in each group, extending over a mean distance of 0.139 mm.

Q. mesomelinus has a significantly greater peg density per unit length than Q. maurus (see above) with up to 3 horizontally adjacent pegs.

Q. skoraszewskyi (Fig. 6.4d-f).

The lateral lobe and peg pattern is of the Q. mesomelinus type and the pattern consists of two vertical elongate groups of pegs which are situated near to the lateral edge at the widest point of the lateral lobe.

There are on average 9.37 (left) : 9.62 (right) peg setae in each group extending over a distance of 0.145 mm, which is longer than Q. mesomelinus and with slightly fewer pegs. The main distinguishing features of Q. skoraszewskyi do not lie in the peg pattern and from this alone it is little different from Q. mesomelinus.

Q. kraussi (Fig. 6.3a-c).

The lateral lobe and peg pattern is of the Q. mesomelinus type but more distinguishable from it than Q. skoraszewskyi. The peg pattern consists of two elongate groups of peg-setae, each group with its apex at the widest point of the lateral lobe, and converging distally, parallel with the converging margins of the lateral lobe.

There are on average 14.5 (left) : 14.3 (right) peg setae in each group, extending over a distance of 0.161 mm.

The peg density per unit length is greater at 0.0109 and significantly distinct from Continental European Q. mesomelinus ($t = 4.813$, $P = 0.05$, 56 d.f.) and there are up to 4 horizontally adjacent pegs.

Q. m. silensis (Fig. 6.3d-f).

Three specimens reveal that the lateral lobe and peg pattern is of the Q. mesomelinus type, with indications that the peg setae

are in two groups one on either side of the lateral lobe at the widest point. The two groups are extremely close to the lateral margins of the lateral lobe.

Q. m. fiorii (Fig. 6.3g).

Two specimens exhibit a lateral lobe and peg pattern of the Q. mesomelinus type.

A more quantifiable pattern analysis is difficult because of the variability in shape of the lateral lobe which does not present a single reference point with which comparisons of all the "species" may be made.

6.8 Proposed status of Q. maurus; Q. mesomelinus and its "varieties"

Q. maurus

Q. maurus is a distinct species distinguishable from Q. mesomelinus and its "varieties" on the basis of numerous characters.

Joy (1932) distinguishes the two by:

"Q. maurus has black elytra with a slight blue reflection more strongly and diffusely punctured than Q. mesomelinus, and smaller in length".

From the results presented here Q. maurus is distinguished by:-

- a) smaller size, reflected in pronotum length and breadth, elytral length and breadth, and median lobe length.
- b) lack of two apical projections on median lobe.
- c) characteristic lateral lobe shape.
- d) longer characteristic peg pattern, giving distinct lateral lobe length/peg pattern length ratio.

Evidence suggests that Q. maurus is sympatric and often syntopic with Q. mesomelinus throughout its range in Britain and Europe, and so the combination of these features maintains the specific integrity of Q. maurus.

Q. skoraszewskyi

From the evidence here, Q. skoraszewskyi is an isolated, high-altitude subspecies of Q. mesomelinus. All locations from which specimens have been received are of similar type. In Austria, the Hochschwab mountains, in the Steiermark region, reach an altitude of 2,278 m and specimens have been examined from 2000 m and also from Kals, a high resort in the middle of a forest near Kalser Valley, Tirol which reaches an altitude of 1,324 m. In Italy all the locations are alpine, San Martino, Tirol, Bressanone, Val Gardena and Alto Adige in the north-west Dolomites and reach altitudes of 1981-3048 m. Locations in Switzerland include Guarda, Lower Engadine (at 1524-1829 m.) and Arosa (at 1000-2000 m.). Czechoslovakia and Bulgarian specimens were similarly from altitudes of around 1219 m.

The distinguishing features of Q. skoraszewskyi compared with Q. mesomelinus are:-

1. Longer median lobe.
2. Lack of apical projections on median lobe (also Q. maurus).
3. Longer apex strut on median lobe.
4. Longer lateral lobe.
5. Distance from base of lateral lobe to base of peg pattern greater.
6. Apex of lateral lobe long and tapering.
7. Shape and position of peg pattern.
8. Median lobe shape.

There are no external features which distinguish Q. skoraszewskyi from Q. mesomelinus.

There is not enough evidence to give Q. skoraszewskyi specific status, even though it is the most distinct "variety" of Q. mesomelinus, because it cannot be determined whether populations of Q. skoraszewskyi and Q. mesomelinus could interbreed.

If Q. skoraszewskyi is geographically isolated it may either be

a true species or an isolated race of Q. mesomelinus.

If Q. skoraszewskyi and Q. mesomelinus overlap at their boundaries it would be necessary to determine whether specific mate recognition and reproductive isolating mechanisms are in operation. Alternatively a transitional form may occur between the common Q. mesomelinus and the alpine Q. skoraszewskyi forming a geographical cline, or the two may be part of a stepped cline. There is no evidence from Q. mesomelinus at locations near to those of Q. skoraszewskyi that such a transitional form exists.

If Q. skoraszewskyi is a distinct species adapted to colder altitude conditions it may be that during the last glaciation it was more widespread over Europe and has now, in a warmer climate, retreated to its present locations. It would be valuable to know whether the populations of Q. skoraszewskyi are connected along mountain chains or whether each population is a relict of a previously widespread species. Information from similar climatic conditions in Scandinavia regarding the presence or absence of Q. skoraszewskyi would be useful.

Q. m. kraussi

Q. m. kraussi is far less distinguishable from Q. mesomelinus than is Q. skoraszewskyi, from which it is easily separated.

Korge (1961) suggests some external distinguishing features:-
"the head is on average barely transverse, more quadrate. The temples are parallel behind the eyes, sometimes slightly widened, whereby the hind angles of the head are distinctly marked. The eyes are smaller, the posterior ocular puncture is more widely distant from the eye and is almost the same distance from the neck edge and the edge of the eye". These are, however, difficult characters and very comparative.

From the results presented here the distinguishing characters from Q. mesomelinus are:-

1. the distance between the apical projections of the median lobe is much smaller.
2. the position of the peg pattern and peg number are characteristic.
3. the apex strut length of the median lobe is longer on average.

Sample means provide distinction from Q. mesomelinus (see earlier) but these are not adequate for use as deterministic characters.

Similar problems arise regarding the state of isolation of Q. m. kraussi. As with Q. skoraszewskyi there is only limited available information on the geographical distribution and habitat preferences. It is likely that Q. m. kraussi is a geographical race of Q. mesomelinus.

Q. m. silensis

Comments are based on observations of three specimens which indicate trends in particular characters in specific directions. There are no characteristic external differences. The principle differences are:-

1. greater distance between apical projections on the median lobe.
2. apex strut of median lobe shorter.
3. apex of lateral lobe of distinct shape.
4. characteristic position and shape of peg pattern.

Q. m. silensis appears to be a southern Italian race of Q. mesomelinus occurring at the end of a geographical cline, which falls outside the range of Q. maurus.

There is a noticeable transition from the common population of

Q. mesomelinus in Continental Europe to Q. m. silensis in southern Italy. This is exhibited by specimens from northern and central Italy which approach Q. m. silensis in those characters listed above.

The mean values for European Q. mesomelinus (which include these transitional forms) for apex strut length and distance between median lobe apical projections are $0.269 \text{ mm} \pm 0.002$ (S.E.) and $0.242 \text{ mm} \pm 0.003$ respectively, for the transitional forms $0.254 \text{ mm} \pm 0.058$ and $0.283 \text{ mm} \pm 0.009$, and for Q. m. silensis $0.282 \text{ mm} \pm 0.031$ and $0.319 \pm 0.014 \text{ mm}$.

Definite conclusions cannot be made owing to the lack of distributional and habit data.

Q. m. fiorii

Again only tentative suggestions can be made and further investigations should bear the following characters in mind.

1. Pronotum length.
2. Elytral length and breadth.
3. Pronotum length/median lobe length.
4. Pronotum length/lateral lobe length.
5. Lateral lobe apex shape.
6. Shape and position of peg pattern.

Q. m. fiorii is probably an isolated race from central and northern Italy adapted to cave dwelling.

6.9 SUMMARY

The geographical variation in genital characters is less than in other external characters and clines in genital characters cannot be directly related to factors which affect the variability of external characters, such as climate.

Analyses of peg patterns prove that there is overall constancy within a species and there is particular stability in range of variation in peg pattern length within all Q. mesomelinus and its races.

Local variants which might be responsible for signal differences (i.e. "dialects") have been investigated to establish whether the genital characters of Q. mesomelinus are less variable in areas of sympatry with Q. maurus. Evidence from Q. mesomelinus populations outside the range of Q. maurus including the Falkland Is., Shetland Is., and Q. m. silensis (from Italy) suggest that outlying populations of Q. mesomelinus are more variable in this respect. In fact, all of the peripherally isolated races of Q. mesomelinus, including Q. skoraszewskyi, probably fall outside the immediate range of Q. maurus, and this may be a factor affecting their variability.

Korge (1961) thought that the Adriatic was the area of origin of Q. mesomelinus which accounted for the variability in that area. There would seem to be no particular evidence to support this view, and the variability of peripherally isolated populations of Q. mesomelinus may have complex origins. The absence of closely related Q. maurus may be one factor.

SECTION 7

PHYLOGENETIC RELATIONSHIPS IN THEPhilonthus sordidus - Group7.1 Staphylininae

The Staphylininae (sensu lato) are a well defined group, the limits of which have been subject to little disagreement among taxonomists. There has been less agreement concerning infra-subfamilial classification and in the past various groups have been defined. For the purpose of the present discussion the subfamily is regarded as comprising 5 tribes, all of which are likely to represent monophyletic groupings (sensu Hennig, 1965). This arrangement follows the provisional phylogenetic hypotheses of A. F. Newton (pers. comm.) (Fig. 7.). The 5 tribes are:-

Platyprosopini (one genus only - Platyprosopus)

Diochini (Diochus (Coiffait & Saiz, 1968; Coiffait, 1972), and

Antarctothius Coiffait & Saiz (1969).

Othiini (sensu Coiffait, 1972)

Xantholinini (sensu Coiffait, 1956)

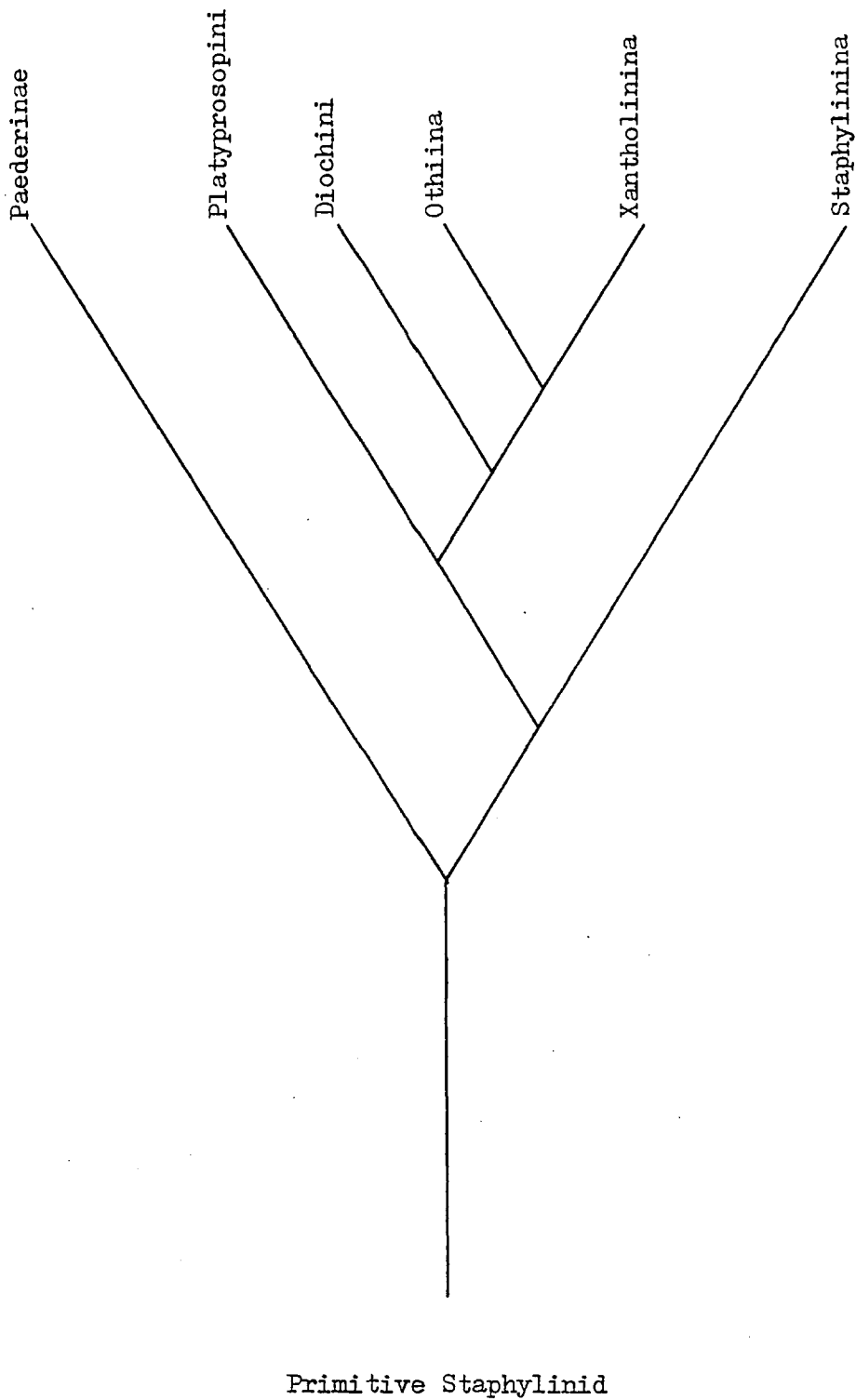
Staphylinini (sensu A. F. Newton (pers. comm.)).

The present review of secondary sexual and genital characters is concerned primarily with the Staphylinini, the largest of the 5 tribes. Discussion of members of this group is prefaced by brief comment on the remaining 4 tribes.

7.1.1. Platyprosopini

The Platyprosopini, sometimes considered as a subfamily, or within the tribe Xantholinini or Staphylinini, comprises a single pantropical genus, Platyprosopus. It is a group of uniform general

Fig.7.1 Provisional reconstruction of phylogenetic relationships
of major staphylinine groups and the Paederinae
(after A.F.Newton, pers.comm.).



structure. The genitalia, which are of a type likely to be primitive in the context of the Staphylininae as a whole, also exhibit little variation of basic structure. The median lobe of all Platyprosopus is bulbous basally and bears a pair of quite separate, long and slender lateral lobes (Coiffait, 1968). The genitalia, at rest, lie without rotation in the abdomen (180° , Coiffait, 1972). As in many male Staphylininae the posterior border of the eighth abdominal sternite is triangularly emarginated. There are, in general, no other striking secondary sexual characters.

7.1.2. Diochini

The Diochini, similarly sometimes considered as a tribe of "Xantholininae" or a subtribe of Xantholinini, are also a group of generally uniform structure. In the tropical genus, Diochus, the genitalia are of the primitive trilobed type (figured by Coiffait & Saiz, 1968 and Coiffait, 1972) and lie at 90° in the abdomen at rest. Striking secondary sexual features are generally lacking.

The genus Antarctothius, from the southern tip of South America, probably also belongs here (Coiffait & Saiz, 1969). In contrast to Diochus the genitalia lie without rotation at rest in the abdomen (180° , Coiffait & Saiz 1969).

7.1.3. Othiini

The Othiini are a Holarctic group with a few representatives in southern temperate zones, notably New Zealand and Chile. They are sometimes considered as a tribe of "Xantholininae". The genitalia are of the primitive trilobed type, but at rest are rotated at 90° in the abdomen and are figured by Coiffait (1972). Striking secondary sexual characters are generally lacking.

7.1.4. Xantholinini

The Xantholinini are a more diverse group, and more specialised in terms of the form of the genitalia. There is considerable development of the basal bulb of the median lobe which has become thick-walled, dorso-ventrally flattened and somewhat purse shaped. The apical portion is reduced in size and generally bears two small lateral lobes, although these may be lost in some species (figured by Coiffait, 1972). The median lobe is not evaginated during mating owing to its size and shape. Only the internal sac, which is elaborate and bears an extensive armature of spines, is extruded. The genitalia lie 180° in the abdomen, i.e. lateral lobes ventral (without rotation, Coiffait, 1972). As with the other four primitive tribes of the subfamily, the Xantholinini generally do not possess elaborate secondary sexual characters on the abdomen or legs.

7.1.5 Staphylinini

The Staphylinini, the largest and most diverse of the tribes of Staphylininae, exhibit a number of genital features which are derived in the context of the subfamily as a whole (Tables 7.1-7.5). Sexual dimorphism is generally greater than in the other tribes, involving, in some cases, the antennae, prothoracic legs, head and pronotum. Except for a few isolated cases the males have the posterior border of the eighth abdominal sternite more or less triangularly emarginate (Fig.4.41). Secondary sexual features involving the posterior legs, and various abdominal segments of males are also to be found in some genera.

None of the various current classifications of the Staphylinini are likely to truly reflect the phylogenetic relationships of the members of this tribe. However, here six subtribes are recognised (A. F. Newton pers. comm.), an arrangement which may approximate more closely to a phylogenetic classification than any other system.

The subtribes Quediina, Amblyopinina, and Holisina, are more likely to represent monophyletic groups. The Xanthopygina probably remains the least satisfactory of the groups, and it is likely that a number of genera placed here (e.g. Creophilus and closely allied genera) will be found to be more closely allied to genera placed in the Staphylinina, than to Xanthopygus and its relatives.

The six subtribes are:-

Xanthopygina (sensu Sharp, 1884) excluding Creophilus

Staphylinina (based on Blackwelder, 1952; Coiffait, 1974) including Creophilus.

Philonthina (based on Blackwelder, 1952; Coiffait, 1974).

Quediina (based on Blackwelder, 1952; Smetana, 1971).

Amblyopinina (Seevers, 1955).

Holisina Holisus and Cephaloxynum.

Some of the principal characteristics of secondary sexual features and genitalia in the subtribes are indicated in Tables (7.1-7.5) which give data for 116 genera. The number of glabrous antennal segments is also indicated as this character is of some value in assessing relationships within the Staphylinini. These comprise all the material which was available for dissection as well as data derived from the literature.

7.1.5.1 Xanthopygina

Tropical genera of the Xanthopygina possess some striking secondary sexual features Table (7.1). Males of Styngetus have crenulate posterior femora while in Hadrotus, Brachydirus and Plociopterus there are modifications of the abdominal sclerites. In Hadrotus the seventh sternite is lobed and in Brachydirus the ninth sternite is extended into a long spine. In Plociopterus the female eighth tergite and sternite may bear specialised setae, while the male

TABLE 7.1

Secondary Sexual Characters of the Xanthopygina

Genus	Position of genitalia in abdomen, in repose	Asymmetry in genitalia	Lateral lobe bifid-b entire-e	Peg setae present+ absent- toothed-t	Other modification	Glabrous antennal segments
Agacerus	90	-	e	-	-	1-3
Agelosus	90	+	e	+	-	1-4(5)
Amelinus	90	-	e	+	-	1-3
Brachydirus	90	-	e	+	♂ 8ST ♂ 9ST	1-5
Eugastus	?	-	e	+	-	1-3
Gastrisus	90	-	e	+	-	1-3
Glenus	90	+	e	+	-	1-5
Hadropinus	90	-	e	-	-	1-5
Hadrotes	90	-	e	-	♂ 7ST	1-5
Liusus	90	-	e	-	-	1-5
Pammegus	90	-	e	+t	-	1-3
Phanolinus	90	-	e	+	-	1-3
Philothalpus	90	-	e	+	-	1-3
Plociopterus	90	-	e	+	♀ 8T ♂ 8T, 8ST, 9ST	1-5
Quediosoma	90	-	e	+	-	1-3
Styngetus	90	-	e	+	♂ hind femora crenulate	1-3
Thinopinus	90	-	e	-	-	1-3
Trigonopselaphus	90	-	e	+	-	1-3
Tympanophorus	?	+	?	+	♂ 7ST	1-4
Xanthopygus	90	-	e	+	♂ 7ST	1-3
Xenopygus	90	-	e	+	-	1-4

TABLE 7.2

Secondary Sexual Characters of the Staphylinina

Genus	Position of genitalia in abdomen, in repose	Asymmetry in genitalia	Lateral lobe bifid-b entire-e	Peg setae present+ absent- toothed-t	Other modification	Glabrous antennal segments
/ Abemus	90	-	e	-	♂ 7ST	1-3
/ Alapsodus	90	+	e	-sp	-	1-3 T.S. <u>morio</u>
/ Atlantogoeus	90	+	e	-	-	1-3 T.S. <u>silvanicus</u>
Barygnathus	?	+	e	?	-	1-3
Craspedomerus	90	-	b	-sp	-	1-3
Creophilus	90	-	e	-sp	-	1-6
/ Dinothenarus	90	+	e	+	-	1-3 T.S. <u>pubescens</u>
Emus	90	-	e	-	♂ 7ST ♂ hind troch.	1-5
Erichsonellus	90	-	e	-	-	1-3
Eucibdelus	90	-	absent	-	-	1-5
Leistotrophus	90	-	e	-	♂ 7ST	1-5
Menoedius	90	+	e	-	♂ 7ST	1-5
/ Metocypus	90	+	e	-	-	1-3
Naddia	90	-	absent	-	♂ 7ST	1-4
/ Ocypus	90	+	e	-	-	1-3 T.S. <u>cyaneus</u>
Ontholestes	90	-	e	-	-	1-4
Palestrinus	90	+	e	+(sm)	-	1-4

TABLE 7.2 (continued)

Secondary Sexual Characters of the Staphylinina

Genus	Position of genitalia in abdomen, in repose	Asymmetry in genitalia	Lateral lobe bifid-b entire-e	Peg setae present+ absent - - toothed-t	Other modification	Glabrous antennal segments
/ Parabemus	90	+	e	+	-	1-3 <u>T.S.fossor</u>
Parapalaestrinus	90	?	?	?	♂ 7ST	1-4
Physetops	90	+	e	-	-	1-4
/ Platydracus	90	+	e	-	-	1-3
/ Protogoerus	90	+	e	-	-	1-3 <u>T.S.brachypterus</u>
/ Pseudocypus	90	+	e	-	-	1-3 <u>T.S.mus</u>
Rhynchocheilus	90	+, -	e	+	♂ 8ST	1-4(5)
Seleucus	90	+	e	+	-	1-3
Staphylinus	90	+	e	+sp	-	1-3
/ Tasgius	90	+	e	-	-	1-4 <u>T.Astrapaeus</u> <u>rufipes</u>
Thoracostrongylus	90	-	e	-	♂ 7ST	1-4
Trichocosmetes	90	+	e	+	-	1-4

T Type specimen

/ Sometimes considered Subgenera of Staphylinus

sm small

sp spicules

T tergite

ST sternite

eighth tergite and sternite are elaborately lobed. The valvulae of the ninth segment are extraordinarily developed and bear patches or rows of peg setae, combs of long asymmetrical peg setae and long stout black tapering setae which are characteristic for individual species (Hammond, 1972a).

The median lobe, which at rest lies in the abdomen at 90° , has an elaborate apical structure in some genera. The lateral lobe is entire and small rounded peg setae, similar to those found in the Philonthina occur in the majority of genera. Agacerus, Thinopinus, Hadrotes, Liusus, and Hadropinus, however, do not possess setae of this type. Asymmetry of the genitalia occurs only in Agelosus and Glemus (Table 7.1). There may be 2, 4, 5, 6 or 8 pairs of apical setae on the lateral lobe with additional shorter setae surrounding these in some genera.

7.1.5.2 Staphylinina

In this subtribe, the males of Ocypus and Emus have secondary sexual modifications of the legs, with stout, prickly setae on the tibiae and the modified shape of the posterior trochanters respectively. Abdominal modifications are also exhibited by Emus and Abemus, where the seventh sternite bears an area of dense pubescence.

The median lobe at rest lies at 90° in the abdomen and exhibits some more specialised features, notably the apex with its asymmetry and striking cuticular processes. The internal sac is well developed with two or three large and well chitinised "copulatory pieces" (Coiffait, 1974).

The lateral lobe is entire in all genera, except Craspedomerus where it is distinctly bifid, but asymmetry is a common feature. Short rounded peg setae of the type found in the Philonthina and many Quediina are present in only a few genera (Table 7.2); in the same position some genera possess series of small tooth-like spicules.

TABLE 7.3

Secondary Sexual Characters of the Philonthina

Genus	Position of genitalia in abdomen, in repose	Asymmetry in genitalia	Lateral lobe bifid-b entire-e	Peg setae present- + absent- - toothed-t	Other modification	Glabrous antennal segments
Actinus	90	-	e(sm)	-	-	1-4
Afrorabigus	?	-	b,e	+	-	1-3 T.P.basilewskyi
Amichrotus	90	+	e	+	-	1-3
Belonuchus	90	-	absent,e	+	♂ fore & hind femoral teeth	1-3
Cafius	90	-	e	+ gr	-	1-3
Chroaptomus	90	-	e(sm)	-	-	1-3
Diatrechus	90	-	e	+ gr	-	1-3
Endeius	0	-	e(sm)	-	-	1-3 T.E.loensis
Erichsonius	90	-	2	+, -	-	1-3
Gabrius	180	-	b,e	+	femora	1-3
Gabronthus	90	-	b,e	+	-	1-3
Hesperopalpus	?	-	e	?	-	1-3
Hesperus	90	-	b,e	+, -	-	1-3
Jurececia	90	-	e	+	-	1-3
Leptopeltus	90	-	absent	-	-	1-3
Leucitus	90	+, -	e(sm)	-	-	1-4
Linoderus	90	-	absent	-	♂ 8ST ♂ head	1-3
Misantlius	90	-	e	+	-	1-3
Musicoderus	0	-	absent	-	♂ fore & hind femoral teeth	1-3
Mysolius	90	-	e(sm)	-	-	1-4

TABLE 7.3 (continued)

Secondary Sexual Characters of the Philonthina

Genus	Position of genitalia in abdomen, in repose	Asymmetry in genitalia	Lateral lobe bifid-b entire-e	Peg setae present- + absent- - toothed-t	Other modification	Glabrous antennal segments
Neobisnius	90	-	b,e	+	-	1-3
Odontolinus	90	-	absent	-	♂ fore femoral teeth	1-3
Onthostygnus	90	-	e	-	-	1-3
Orthidus	90	-	e	+	-	?
Paederomimus	90	-	absent	-	♂ fore femoral teeth	1-3
/Palaeophilonthus	180	-	2	+	-	1-3
/Paragabrius	180	-	b,e	+	-	1-3
Philonthus	90	+, -	b,e	+, - gr	-	1-3
Phucobius	90	-	e	+	♂ 7ST	1-3
/Rabigus	90	-	e	+	-	1-3
Remus	90	-	e	+	-	1-3
/Spatulonthus	0	-	e	+	-	1-3
Stevensia	90	-	b,e	+	-	1-3
Thinocafius	?	-	e	+	-	1-3
Tolmerinus	90	-	b,e	+	-	1-3

/ Subgenera of Philonthus

sm small

gr grouped

T Type specimen

These may be a form of peg setae. There are usually 2-4 pairs of apical setae on the lateral lobe, frequently with a number of shorter setae around the apical edge.

7.1.5.3 Philonthina

In the Philonthina elaborate secondary sexual characters of the legs are notable only in Gabrius where the posterior femora and tibiae may be toothed and possess fringes of setae.

The median lobe at rest is rotated through 90° in the abdomen in the majority of genera; however, in Gabrius and Paragabrius (often regarded as a sub-group of Philonthus) it is rotated through 180° (without rotation, Coiffait, 1974), and in some Philonthus (e.g. subgenus Spatulonthus) Endeius and Musicoderus it lies in the primitive position for the Staphylinidae as a whole (180° , Coiffait, 1974) (Section 7.1.6) (Table 7.3).

The basic structure of the median lobe is uniform throughout the group although variation in the apex may be considerable and may bear cuticular ridges or teeth on the surface facing the lateral lobe: Orthidus is an extreme case where the median lobe is divided into dorsal and ventral lobes.

Separate lateral lobes resembling those in the more primitive tribes are found in Erichsonius.

Two separate lateral lobes also occur in the genus Palaeophilonthus. This genus was erected by Coiffait (1972) for one species, P. rossicus, based on a single male specimen from Vologda, Russia. P. rossicus was first assigned to the genus Sectophilonthus (Coiffait, 1965) of which the clearly rather distantly related S. biparamerosus Tott., described from Madagascar, is the type. All the features of P. rossicus, apart from the genitalia, are those of Philonthus decorus and as the genitalia exhibit signs of abnormal development it is likely that its unusual characteristics are teratological

TABLE 7.4

Secondary Sexual Characters of the Quediina

Genus	Position of genitalia in abdomen, in repose	Asymmetry in genitalia	Lateral lobe bifid-b entire-e	Peg setae present - + absent- - toothed-t	Other modification	Glabrous antennal segments
Acylophorus	90	-	b+e	+	-	1 (1-3)unclear
Algon	90°	-	e	+4	-	1-3
/Anaquedius	(90)	-	e	+ gr	-	1-3 T.Q. <u>vernix</u>
Anchocerus	90°	-	absent	-	-	1-3
Astapaeus	90°	-	e	-	-	1-3
Atanygnathus	90	-	absent	-	♂ fore femoral brush	all (1-3) pubescent unclear
Cafoiquedius	180°-90°	-	e	-	-	1-3
Cheilocolpus	90°	?	e	-	-	1-3
Cordylaspis	90°	-	e	-	-	all glabrous, pubescence at sides
Cyrotothorax	90°	-	b	+	-	1-5
Euryporus	90°	-	e	+	-	1-3
Haemotodes	90	-	e	+ gr	♂ 7ST setal brush	all glabrous, pubescence at sides
Hasumius	90	-	e	+t	-	1-3
Heinzia	?	-	e	+	-	1-3
/Hemiquedius	(90)	-	suture e	+ gr	-	1-3 T.Q. <u>ferox</u>
Heterothops	90	-	absent	-	-	1-3

TABLE 7.4 (continued)

Secondary Sexual Characters of the Quediina

	Position of genitalia in abdomen, in repose	Asymmetry in genitalia	Lateral lobe bifid-b entire-e	Peg setae present - + absent - - toothed-T	Other modification	Glabrous antennal segments
Loncovilius	90°	-	e	+t	-	1-3
Moecerus	90	-	e	-	-	1-3
Myotyphlus	?	?	e	-	?	1-3
Pseudorientis	?	?	?	+	?	1-3
Quedimacrus	90	-	e	+ gr	-	1-4
Quedionuchus	(90)	-	e	+	-	1-3 T.Q. <u>impunctus</u>
Quediopsis	(90)	-	e	+	-	1-3 T.Q. <u>riparius</u>
Quedius	90	-	e	+	-	1-3
Sphingoquedius	90	-	e	+ t	-	1-3
Termitoquedius	90	?	e	?	?	1-3
Triacrus	90	+	e	+	-	1-4
Velleius	90	-	b + e	+	-	1-3

/ subgenera of Quedius
gr grouped

(Crowson, 1970).

In all other genera of Philonthina the lateral lobe is entire, although it may be bilobed in some (Table 7.3). Asymmetry in the lateral lobe is exhibited by some species of Philonthus, notably in the sub-genus Spatulonthus.

Most species of all genera possess small rounded peg setae on the lateral lobe. Exceptions, which are few, are found in Erichsonius, Hesperus, and Philonthus, (Table 7.3), and all have 2-4 pairs of apical setae.

7.1.5.4 Quediina

Close to the Philonthina are the Quediina. Notable male secondary sexual characters on the legs are exhibited only by Atanygnathus, (Table 7.4), where there is a setal brush on the inside of the anterior femur. The posterior border of the eighth sternite is triangularly emarginated in most genera, but there are exceptions (e.g. Acylophorus, Hemiquedius and Anaquedius). The median lobe, particularly the apical structure, is very important in species determination; many bear cuticular projections on the surface facing the lateral lobe (e.g. Quedius mesomelinus). At rest the median lobe lies at 90° in the abdomen.

The lateral lobe is entire, although in some genera it may be more or less bilobed (e.g. Cyrtothorax, Table 7.4), or with a mid-line suture (e.g. Hemiquedius), while in Heterothops the lateral lobe is absent. The apex of the lateral lobe may be elaborately thickened bearing hook-like processes (e.g. Cheilocolpus) (Coiffait & Saiz, 1966) and Myotyphlus).

Peg setae on the lateral lobe are present in most genera in the short and rounded form typical of the Philonthina; however, small short tooth-like peg setae similar to those in the Amblyopinina and spicules of Staphylinina, are found in Loncovilius, Quediopsis

and Hasumius (Table 7.4). Lateral lobe peg setae are absent in Atanygnathus, Cheilocolpus, Sphingoquedius, Cafioquedius and Myotyphlus. Apical setae range from 2-4 pairs often with many smaller setae around the lateral edges of the lateral lobe. The internal sac may exhibit very elaborate armature (e.g. Heterothops and Atanygnathus Smetana, 1971).

7.1.5.5 Amblyopinina

The Amblyopinina are a highly specialised group which are obligate ecto-parasites on rodents and marsupials in the subtropical and temperate regions of the Neotropics. The group may have a close affinity to the Quediina.

There is an entire lateral lobe often with an elaborate apical development and bearing tooth-like peg setae which resemble those of some Quediina and Staphylinina. The apex of the median lobe and developed internal sac armature are important for species determination (Seevers, 1955; Machardo Allison, 1962a&b). The genitalia lie at 90° in the abdomen at rest (Table 7.5).

7.1.5.6 Holisina

There is no published information on the Holisina, and specimens of Cephaloxynum and Holisus were not available for examination.

7.1.6 Polarity of character states relating to male

Staphylinini genitalia and secondary sexual characters.

The significance for phylogenetic classification of the characters surveyed in Tables 7.1-7.5 may be clarified by an assessment of their plesiomorphic and apomorphic states (Table 7.6). This is a necessary preliminary to any attempts to reconstruct the phylogenetic relationships of the subtribes and their genera and also acts as a background to later work on a specific group within the Philonthina, the Philonthus sordidus-Group (7.2).

TABLE 7.5

Secondary Sexual Characters of the Amblyopinina

Genus	Position of genitalia in abdomen in repose	Asymmetry in genitalia	Lateral lobe bifid-b entire-e	Peg setae present- + absent- - toothed-t	Other modification	Glabrous antennal segments
Amblyopinodes	90		e	+ t		1-3
Amblyopinus	90 -		e	+ t		1-3
Edrabijs	90		e	+ t		1-3

Much of the data can be applied to the Staphylininae as a whole but relates more specifically to the states within the Staphylinini. The list is based on experience of the Staphylininae as a whole and the plesiomorphic and apomorphic states are assessed according to the distribution of characters, their frequency of occurrence, functional significance, their state of development and correlation of series of transformations; geographical, ecological, cytological and geological information could also be used if available (Hennig, 1966).

The apomorphic states in characters 6, 10, 13, 14 and 15 (Table 7.6) are based upon their comparative rarity of occurrence within the subfamily as a whole. The apomorphic states in characters 2, 4, 5, 8, 9 and 12 exhibit an advanced development of a more conservative condition. The apomorphic states of characters 7 and 11 do not occur in the Xantholinini, Diochini, Othiini and Platyprosopini which are considered to be primitive in the context of the subfamily as a whole.

Despite Coiffait's (1972, 1974) acceptance that a position with the lateral lobes ventral in the abdomen is the primitive condition for staphylinid male genitalia, a survey of the resting position throughout the Staphylinidae appears to indicate otherwise. This is also surveyed by Tikhomirova (1973). The lateral lobes of the male genitalia in repose in the abdomen are dorsal in all members of the primitive subfamily Omaliinae, in at least the primitive members of other subfamilies, such as the Oxytelinae and Tachyporinae, in the Euasthetinae and Steninae, and in many Paederinae (Tikhomirova, 1973, Fig. p. 72). A rotation of 90° is found in representatives of a number of groups, Tachyporinae, Oxytelinae, Paederinae and Staphylininae, and is generally associated with developments in the form of the genitalia and/or abdomen which preclude

convenient positioning of the genitalia in any other way. Dorso-ventral flattening of the abdominal apex is incompatible with symmetrical positioning of genitalia which are at all broadened dorso-ventrally.

The 90° rotation of the genitalia is found almost throughout the Staphylinini, with the exception of groups of Philonthus, Spatulonthus and Paragabrius, where in the former two the genitalia lie with the lateral lobe in a dorsal position, and in the latter, in a ventral position in the abdomen at rest. In Gabrius the lateral lobe lies in the ventral position, whilst in Endeius the lateral lobe is in the dorsal position. This position is generally associated with dorso-ventral flattening of the genitalia.

In the rest of the Staphylininae dorsal lateral lobes are found only in the Platyprosopini and some Diochini, while in the Xantholinini the median lobe is considerably dorso-ventrally flattened and is unable to extrude from the abdomen (or rotate in the process) during intromission and the lateral lobes lie in the ventral position.

In the Staphylininae, when the genitalia are extruded during mating, the lateral lobes are in a ventral position. The abdomen is then curved ventrally bringing the lateral lobes into a dorsal position just prior to insertion of the median lobe into the female genital orifice. A ventral position of the lateral lobes in repose in the abdomen would not require any rotation of the genitalia upon extrusion, whereas those in a dorsal position at rest would require a rotation of 180° . Rotation of the genitalia from the primitive position where the lateral lobes, in repose, lie in the dorsal position seems therefore to be associated with a change in shape of the median lobe or apex of the abdomen and may consequently affect the mating position as in the Xantholinini.

TABLE 7.6

PLESIOMORPHIC AND APOMORPHIC CHARACTERSTATES OF MALE STAPHYLININI GENITALIAAND SECONDARY SEXUAL CHARACTERS

<u>CHARACTER</u>	<u>CHARACTER STATE</u>	
	<u>PLESIOMORPHIC</u>	<u>APOMORPHIC</u>
<u>THORAX</u>		
1. LEGS, EXCLUDING EXPANSION OF FORE TARSUS	AS IN FEMALE	STRUCTURALLY DISTINCT FROM ♀
<u>ABDOMEN</u>		
2. VENTRAL ABDOMINAL SEGMENTS	EMARGINATION OF 8ST	MODIFICATION OF OTHER SEGMENTS
<u>GENITALIA</u>		
3. POSITION OF GENITALIA IN ABDOMEN AT REST	LATERAL LOBES DORSAL, 0°.	(a) 90° ROTATION (a') 180° ROTATION (VENTRAL)
4. SHAPE OF GENITALIA	SYMMETRICAL	ASYMMETRICAL
5. MEDIAN LOBE APEX	SIMPLE	ELABORATE
6. LATERAL LOBE/S	PRESENT	ABSENT
7. CONDITION OF LATERAL LOBE/S	TWO SEPARATE	ENTIRE (FUSED)
8. LATERAL LOBE SHAPE	BIFID	(a) ENTIRE (a') BIFID (a')ii TRI-LOBED (a')iii QUADRI-LOBED
9. LATERAL LOBE APEX	SIMPLE	ELABORATE
10. LATERAL LOBE SIZE	ABOUT AS LONG AS MEDIAN LOBE	SMALL AND MUCH SHORTER THAN MEDIAN LOBE
11. LATERAL LOBE PEG SETAE	ABSENT	(a) PRESENT (a') ABSENT
12. POSITION OF PEG SETAE	AROUND LATERAL LOBE APEX MARGIN	CLUMPED OR REMOVED FROM MARGIN
13. PEG SETA SIZE	≈ 1.2μ x 1.8μ	(a) CONSIDERABLY LARGER (b) CONSIDERABLY SMALLER
14. PEG SETAE SHAPE	APEX ROUNDED	APEX TAPERED
15. PEG NUMBER	≈ 15-25	(a) MUCH < 15 (b) MUCH > 25

7.2 Philonthus sordidus-Group

Results of detailed studies on the mating behaviour of Philonthus sordidus and P. cephalotes, a pair of apparently closely related and syntopic species, have already been discussed (Section 5.21). Despite the close relationship of the species, one of them (P. cephalotes) exhibits characteristics of the male genitalia which are unusual, notably the arrangement of peg setae on the lateral lobe. These are thought to be concerned with specific mate recognition and hence such divergence is not necessarily likely to be an indicator of more distant relationship. Marked divergence from the more usual pattern found in P. sordidus also occurs in a western European species, P. sparsus, which is closely allied to, and syntopic with P. sordidus.

In order to assess the closeness of the relationship between these species and others, which have already been studied with regard to their secondary sexual characters, geographical distributions, habitats, and mating behaviour, material of all species which appeared from descriptions to be at all closely related to P. sordidus was obtained and examined.

As a result of a survey of the literature and examination of all available material of the genus Philonthus in the collection of the BMNH (including the valuable C.E. Tottenham collection), 24 species were identified as likely members of one monophyletic group, here referred to as the Philonthus sordidus-Group.

Their similarities have been assessed using a computer programme to produce a phenetic classification which may form a basis from which some conclusions on phyletic groupings can be made.

Some species previously considered to be closely related to P. sordidus by some authors, are here excluded from the Group, while some of the species included here have not previously been regarded

as at all closely related to the other species of the Group.

Table 7.7 lists the material examined. Specimens of some species unrepresented in the BMNH collections were borrowed for study from other collections, namely:-

Field Museum of Natural History, Chicago	FMNH
H. Coiffait coll. (Toulouse).	C
Naturhistorisches Museum, Vienna	NM
Institut Royal des Sciences Naturelles de Belgique, Brussels	IRSNB
A. Smetana coll. (Ottawa)	S
G. Brunne coll. (Hamburg).	B

The western Palaearctic species which are considered, in the present thesis, to be part of the P. sordidus-Group, have previously been classified into a number of groups on the basis of characters of the lateral lobe (Coiffait, 1963; 1967). Most of the species were placed in the "intermedius-Group" (Coiffait, 1963) along with other species dissimilar in a variety of respects. These species were grouped together owing to the common possession of a lateral lobe with 4 pairs of marginal setae, outside a series of peg setae which are positioned near to the extremity of the lateral lobe. P. subuliformis and P. sparsus were separated into different groups on the basis of the type of peg pattern (Coiffait, 1963) although P. subuliformis was later (Coiffait, 1967) incorporated into the "intermedius-Group", P. sparsus remaining alone in the "sparsus-Group".

P. phaeophilus, P. psyllophagus, P. palmi, P. baicalensis, P. fuentei, P. agyrtes, P. friebi, and P. eidmanni were not examined by Coiffait and remained unplaced.

Coiffait's groupings based on characters of the lateral lobe alone, specifically the positioning of peg setae, clearly contain artificial elements, and are unlikely in many cases to reflect

TABLE 7.7 Material of Philonthus species examined.

HT : Holotype

PT : Paratype

<u>Species</u>	<u>Material Examined</u>	<u>Source</u>
agyrtes Smet.	not seen	Ref. Smetana (1966), (1973)
negligens Smet.	1 ♀	BMNH
baicalensis Ganglb.	PT ♂	C
batkhizensis Coiff.	not seen	Ref. Coiffait (1967)
bucharensis Coiff.	many, ♂ + ♀	BMNH
cephalotes (Grav.)	HT ♂	NM
eidmanni Scheerp.	HT ♂ + 6 ♂ + ♀	BMNH
fletcheri Cam.	PT ♂	BMNH, Ref. Smetana (1967)
friebe Cam.	not seen	Ref. Roubal (1909)
fuentei Roubal	HT + 1 ♂	BMNH
kashmiricus Cam.	PT + 1	BMNH
microtophilus Coiff.	many, ♂ + ♀	BMNH
nigriventris Thoms.	HT ♂ + 2 PT	IRSNB
noualhieri Fauvel	HT ♂	S
palmi Smet.	HT + many, ♂ + ♀	BMNH
parcus Sharp	not seen	Ref. Kirschenblatt (1950), Smetana (1963a)
pholeophilus Kirsch.		
protenus Schub.		
yatungensis Cam.	HT ♀ <u>P.yatungensis</u> + 15 ♂ + ♀	BMNH
pseudoparcus Brunne	many, ♂ + ♀	BMNH, B.
psyllophagus Kirsch	not seen	Ref. Kirschenblatt (1933)
scribae Fauvel	many, ♂ + ♀	BMNH
* sordidus (Grav.)	many, ♂ + ♀	BMNH
pachycephalus (Nordm.)		

TABLE 7.7 (continued)

<u>Species</u>		<u>Material Examined</u>	<u>Source</u>
sparsus Lucas	Figs. 7.2n, 7.4e, 7.6f	many, ♂ + ♀	BMNH
spemophili Ganglb.	Figs. 7.2q, 7.4f, 7.6g	many, ♂ + ♀	BMNH
subuliformis (Grav.)	Figs. 7.2p, 7.4g, 7.6h	many, ♂ + ♀	BMNH
fuscus (Grav.)			
anguinus Fauvel		HT ♀	IRSNB
diversipennis Bernh.		3 ♂ + ♀	BMNH
diversus Schub.		1 ♂	BMNH
fimetarius Grav.		many, ♂ + ♀	BMNH
macies Sharp		HT + 4 ♂ + ♀	BMNH
pentheri Ganglb.	Figs. 7.2q, 7.4h, 7.5k	not seen	Ref. Coiffait (1967)
plagiatus Fauvel		many, ♂ + ♀	BMNH
potanini Epp.	Figs. 7.2r	not seen	Ref. Eppelsheim (1889), Coiffait (1967)
propinquus Kirsch.		not seen	Ref. Kirschenblatt (1950), Coiffait (1974)
scoticus (Joy and Tomlin)		HT + many, ♂ + ♀	BMNH
semiaenescens Bernh.		11 ♂ + ♀	BMNH
siegwaldi Mannerh.		many, ♂ + ♀	BMNH
sogdianus Kirsch.	Figs. 7.2s, 7.4i, 7.5l	not seen	Ref. Kirschenblatt (1950), Coiffait (1967)
sordidioides Scheerp.		PT ♂ + ♀, + 2♀	NM

Footnote

* Staphylinus sordidus Grav. 1802 is not a junior primary homonym of S. sordidus Marsham 1802 as has been thought by some authors, Gravenhorst's work having appeared before that of Marsham. There is therefore no need to replace the well known name of Philonthus sordidus (Grav.) by P. pachycephalus (Nordm.) as some authors have done, e.g. Coiffait.

phylogenetic relationships.

In a morpho-metric study on P. sordidus, P. sparsus, P. spermophili, P. parvus, P. pseudoparvus and P. agyrtes, Brunne (1976) includes all of these species in what he terms the "Philonthus sordidus Group". The group as envisaged here is essentially an extension of Brunne's concept.

Table 7.8 lists the species and outlines their geographical distribution and habitat. Species of the Group are found in a wide range of fragmented habitats including rotting vegetation, compost, dung, carrion and other decaying organic debris. A number of species are found frequently in, and in some cases, are more or less restricted to the nests of birds or small mammals.

Distributional data is such that definite cases where species are syntopic can be singled out in only a few cases:-

P. sordidus + P. cephalotes
P. sordidus + P. nigriventris
P. sordidus + P. parvus
P. cephalotes + P. sparsus

It can, however, be safely predicted that those sympatric western European species with a wide range of habitats are likely to be syntopic, and the same is likely to be true of several of the Oriental species.

Some uncertainty must be expressed concerning the status of two species placed in the group, P. agyrtes and P. palmi.

P. agyrtes (Smetana, 1966) is based on a single male specimen from Bressanone, northern Italy which is indistinguishable in all external characters except the emargination of the posterior margin of the eighth sternite, and the form of the genitalia from P. sordidus. This specimen may well be an abnormal individual

TABLE 7.8

Geographical distribution and habitat
preferences of the *Philonthus sordidus*-Group

	<u>Geographical Distribution</u>	<u>Habitat</u>
agyrtes	N. Italy (Smetana, 1966)	Compost
baicalensis	L. Baikal, Turanskaya (Coiffait, 1974)	-
batkhizensis	"Turkmenia" (Coiffait, 1974)	-
bucharensis	Kirghistan, Uzbekistan (Coiffait, 1974)	-
cephalotes	Holarctic (Horion, 1965)	Wide range of fragmented habitats. Synanthropic.
eidmanni	N.E. China (Scheerpeltz, 1929)	Carcass
fletcheri	N. India (Cameron, 1943)	-
friebei	Mongolia, "Transbaikal" (Smetana, 1967)	<u>Milvus</u> nest: under stone
fuentei	Spain (Coiffait, 1974)	-
kashmiricus	Kashmir (Cameron, 1932)	-
microtophilus	Armenia (Coiffait, 1974)	Especially <u>Microtus</u> nests.
nigriventris	N. & C. Europe, E. to Siberia (Horion, 1965)	Wide range of fragmented habitats
noualhieri	S. Algeria & Morocco (Coiffait, 1974)	-
palmi	Sicily (Smetana, 1954)	-
parcus	Sub-cosmopolitan (Tottenham, 1967; Sharp, 1874; Brunne, 1971)	Range of habitats, especially Chicken dung. Synanthropic
pholeophilus	Amur d., d. Baikal, Mongolia (Smetana, 1963a; Coiffait, 1974)	Especially under- ground nests of <u>Citellus</u> and <u>Marmota</u>
protenus	N. India	Range of habitats, including dung.
pseudoparcus	Britain, Germany, Scandinavia (Brunne, 1976; BMNH coll.)	Range of habitats, especially woodland areas

TABLE 7.8 (continued)

	<u>Geographical Distribution</u>	<u>Habitat</u>
psyllophagus	Mongolia, "Transbaikal" (Coiffait, 1974)	Especially underground nests of <u>Citellus</u> and <u>Microtus</u>
scribae	C. Europe, E. to Kazakhstan (Horion, 1965)	Especially underground nests of small mammals.
sordidus	Sub-Cosmopolitan (Horion, 1965)	Wide range of fragmented habitats. Synanthropic
sparsus	W. Europe, W.N. Africa (Horion, 1965)	Wide range of fragmented habitats. Synanthropic
spermophili	C. Europe - S. Russia (Horion, 1965)	Especially nests of small mammals
subuliformis	Palaeartic (Horion, 1965)	Especially nests of birds, in hollow trees
macies	Japan	-
pentheri	Asia Minor, Armenia	Especially nests of small rodents
plagiatus	N. Africa: Algeria & Libya	-
propinquus	E. Siberia	-
sogdianus	Uzbekhistan	-

of P. sordidus.

P. palmi (Smetana, 1954) is based on a single male specimen from Sicily which is very similar to P. cephalotes, but with some deviant characteristics. These are the very large squared head, the microsculpture of the head which forms oblique waves, the sinuated postero-lateral border of the pronotum, the short elytra, the elytral sculpture and the form of the genitalia.

Specimens of P. sordidioides Scheerpeltz (1962) were examined:-

PT ♂ Rustenburg Transvaal "Im nest des Geirs Gyps coprotheres" dissected.

PT ♀ Rustenburg

2♀ S. Africa Cape Province Suldanhabaai, Jutten Island.

These and other South African specimens in BMNH cannot be distinguished from specimens of P. sordidus from Europe and other parts of the world. P. sordidioides is regarded here as synonymous with P. sordidus.

Species previously considered to be part of the group by some authors have been excluded here. The reasons for their exclusion are listed below for each species:-

P. alaiensis Coiff.

Note: Inter-ocular punctures equidistant

1. Antennal segments 6-10 elongate.
2. Eyes very small; considerably smaller than the average size for the group - just shorter than the temples.
3. Head and pronotal microsculpture considerably interrupted into very short lengths as in P. semiaenescens. (Plate 7.1)
4. Lateral lobe bifid.

P. anguinus Fauv.

Note: Inter-ocular punctures not equidistant, central two are further apart.

1. Eyes very small as P. alaiensis.
2. Shape of head distinct in female seen, very broad and square

3. Form of genitalia unknown.
4. Inter-ocular punctures not level, (2) more anterior than (9) (Fig. 7.7).

P. diversus Schub.

Note: Inter-ocular punctures not equidistant, central two closer together.

1. Pronotal microsculpture like P. alaiensis.
2. Lateral lobe bifid, dorsally situated at rest in the abdomen (i.e. without rotation), median lobe broad.

P. diversipennis Bernh.

Note: Inter-ocular punctures equidistant.

1. Post-ocular punctures numerous.
2. Lateral lobe bifid, dorsally situated at rest in the abdomen, median lobe broad.
3. Head (chaetotaxy) with many additional punctures.

P. fimetarius Grav.

Note: Inter-ocular punctures not equidistant, central two are further apart.

1. Eyes very small as P. alaiensis.
2. Head and pronotal microsculpture as P. alaiensis.
3. Lateral lobe distinctive (Fig.4.31e), median lobe broad.
4. Head chaetotaxy: extra puncture near to (8) (Fig. 7.7).

P. potanini Epp.

Note: Inter-ocular punctures equidistant.

1. Overall body size very small.
2. Antennal segments 6-10 very transverse.
3. Eyes very small as P. alaiensis.
4. Head and pronotum lacking microsculpture.

5. Lateral lobe bifid, median lobe broad.

P. semiaenescens Bernh.

Note: Inter-ocular punctures not equidistant, central two closer together.

1. Eyes large, larger than temples.
2. Head and pronotal microsculpture like P. alaiensis.
3. Legs testaceous.
4. Lateral lobe bifid, dorsally situated at rest in the abdomen, median lobe broad.
5. Abdominal microsculpture lines very close, compared with P. sordidus less than half as close.

P. scoticus (Joy and Tomlin)

Note: Inter-ocular punctures not equidistant, central two closer together.

1. Post-ocular punctures numerous.
2. Eyes very small, as P. alaiensis.
3. Lateral lobe bifid, dorsally situated at rest in the abdomen, median lobe broad.
4. Abdominal microsculpture lines very close as P. semiaenescens.

P. siegwaldi Mannerh.

Note: Inter-ocular punctures almost equidistant.

1. Five punctures in the pronotal discal series.
2. Post-ocular punctures numerous.
3. Legs testaceous.
4. Lateral lobe bifid, dorsally situated at rest in the abdomen, median lobe broad.

The following five species may be part of the P. sordidus-Group but they possess some characters which are unusual. These are marked*. For this reason they are not included in the phenetic

classification.

P. macies

*Note: Inter-ocular punctures not equidistant, central two are further apart.

1. Antennal segments 6-10, slightly transverse.
2. Eyes just shorter than temples, as usual for P. sordidus-Group.
- *3. Pronotum very narrowing towards apex.
4. Elytral punctures, dense and deep.
- *5. Numerous post-ocular punctures.
6. Microsculpture of head and pronotum distinct, uninterrupted and completely covering the dorsal surface. Branching very frequent; individual lines with a tendency to be "wavy" of the type found in P. eidmanni.
7. Genitalia of P. sordidus-Group type; lateral lobe entire with peg pattern divergent from the common P. sordidus type resembling that of P. cephalotes.

P. pentheri

1. Antennal segments 6-10, transverse.
- *2. Eyes longer than temples, not usual in P. sordidus-Group.
3. Elytral punctures, medium dense and deep.
4. Genitalia of P. sordidus-Group type; lateral lobe entire with peg pattern similar to P. sordidus (Figs. 7.2q, 7.4h & 7.5k).

P. plagiatus

*Note: Inter-ocular punctures not equidistant, central two further apart.

1. Antennal segments 6-10, transverse.
- *2. Eyes longer than temples, not usual in P. sordidus-Group.
3. Elytral punctures, medium dense and deep.
4. Head microsculpture partially interrupted, completely covering dorsal surface.

5. Pronotal microsculpture; centre of dorsal surface devoid of sculpture.
6. Genitalia of P. sordidus-Group type; lateral lobe entire with peg pattern similar to P. sordidus.

P. sogdianus

- *1. Antennal segments 6-10, elongate, not usual in P. sordidus-Group.
- *2. Eyes longer than temples, not usual in P. sordidus-Group.
3. Elytral punctures sparse and fine.
4. Genitalia of P. sordidus-Group; lateral lobe entire with peg pattern similar to P. sordidus (Figs. 7.2s, 7.4i, 7.5l).

P. propinquus

*Note: Inter-ocular punctures not equidistant, central two are further apart.

Coiffait (1974) places P. propinquus near to P. pentheri.

7.2.1 Characteristics of the P. sordidus-Group

1. Eyes as long as, or just shorter than the temples.
2. Head chaetotaxy of basic pattern, (Section 7.2.1.1)
3. Inter-ocular punctures more or less equidistant.
4. Antennae short.
5. Head and pronotal microsculpture defined, (Section 7.2.1.2).
6. Four punctures in pronotal discal series.
7. Elytral punctures never abutting.
8. First posterior tarsal segment short; shorter than the fifth, or as short as tarsal segments 2-4 together.
9. Abdominal pubescence sparse; puncturation sparse.
10. Lateral lobe entire spatulate, long, but never longer than median lobe; with 4 pairs of comparably situated apical setae.
11. Median lobe as broad as, or slightly broader than lateral lobe; both symmetrical.

12. Total body length generally not exceeding 8mm, and not less than 4mm.
13. Body shape characteristic (Plate 5.1)
14. Sexual dimorphism of the fore parts; male often with larger head and pronotum; fore tarsi not generally expanded.
15. Genitalia, in repose, at 90° in the abdomen.

7.2.1.1 Chaetotaxy

The chaetotaxy of the pronotum is rather uniform within the group of Philonthus species which possess 4 punctures in the discal series.

The principle setiferous punctures are figured Fig. 7.7a, other minor punctures may be present in variable positions around the extreme edge. Individual variation within a species may occur in the main punctures, sometimes one may be displaced or lacking, particularly those in the discal series.

The chaetotaxy of the head is of greater importance in distinguishing groups of species. The P. sordidus-Group is characterised by the basic pattern of principal setiferous punctures in Fig. 7.7b.

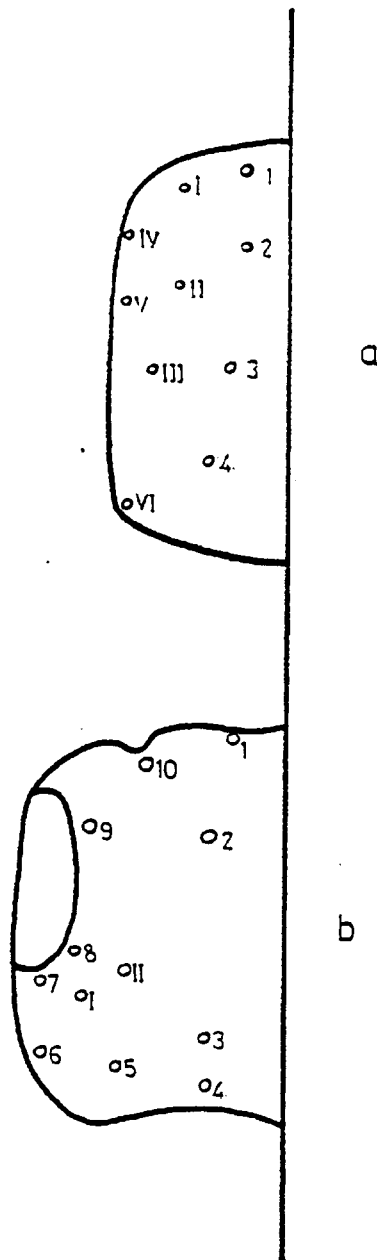
Punctures (9) and (2) are termed the inter-ocular punctures. Punctures (3), (4), (5), (6), (7), I & II are termed post-ocular punctures. The inter-ocular punctures are equidistant and in a straight line. Punctures I and II while always present are somewhat variable in position; I may occur either anterior, posterior or level with II, and II may be more proximal or distal to (8). Accessory post-ocular punctures may be present, but these are generally few in number in the P. sordidus-Group and variable in position in different individuals of the same species.

In other groups of Philonthus, the position of (2) varies in

Fig.7.7. Chaetotaxy of the Philonthus sordidus-Group;

a) pronotum

b) head



relation to (9), additional punctures may occur in the area of (7), I and II and further post-ocular punctures may be characteristic of individual species.

7.2.1.2 Microsculpture

The dorsal surface of the head and pronotum are more or less covered with a transverse reticulate microsculpture which is present in varying degrees of completeness in different species. Transverse sculpture of this kind is widespread in the Staphylinina but different forms can be distinguished (e.g. P. semiaenescens, Plate 7.11), which characterise a group of species including P. fimetarius, P. alaiensis and P. diversus; and P. cephalotes, which exhibits one of the forms of microsculpture which characterises the P. sordidus-Group.

In its most complete form, in the P. sordidus-Group, the transverse lines are well defined, branching at frequent intervals and cover the entire surface of the head and pronotum (e.g. P. nigriventris, Plates 7.2 & 7.8). At its most incomplete both the head and pronotum may be entirely devoid of microsculpture leaving a shining surface. All stages between these two extremes are exhibited by individual species. The centre of the dorsal surface of the head or pronotum may be smooth and devoid of microsculpture, rudiments of sculpture being visible only at the outer edges. Alternatively, the entire dorsal surface may be covered in a much more interrupted form, with short lines of sculpture and few complete visible branches; again the outer edges may be more complete.

Often the head and pronotum do not exhibit the same condition of sculpture; that on the surface of the head is generally more complete. The distance between the lines of sculpture may be characteristic of individual species.

Hinton (1970) discusses forms of microsculpture in insects, the

Plates 7.1 - 7.6. Scanning electron micrographs of Philonthus head
microsculpture. (x 600).

7.1 P.subuliformis

7.2 P.nigriventris

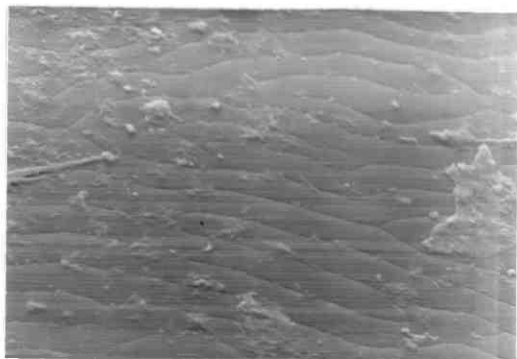
7.3 P.parcus

7.4 P.protenus

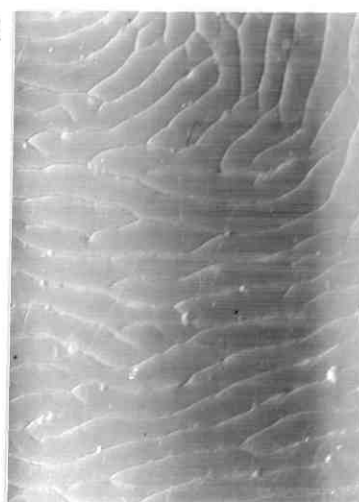
7.5 P.semiaenescens

7.6 P.spermophili

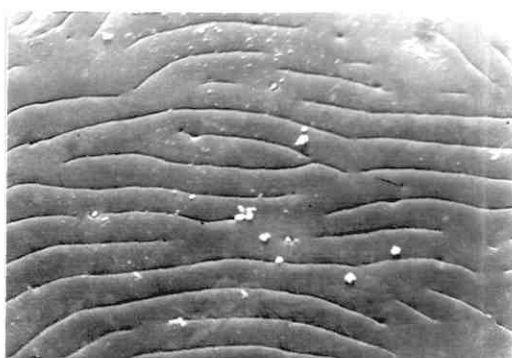
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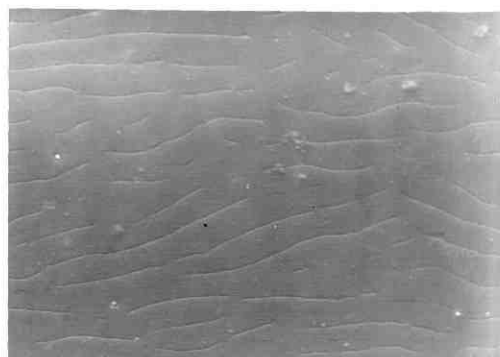
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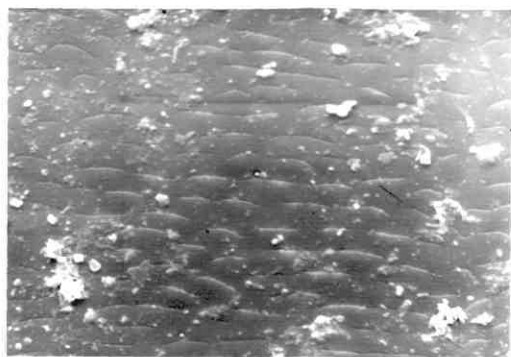
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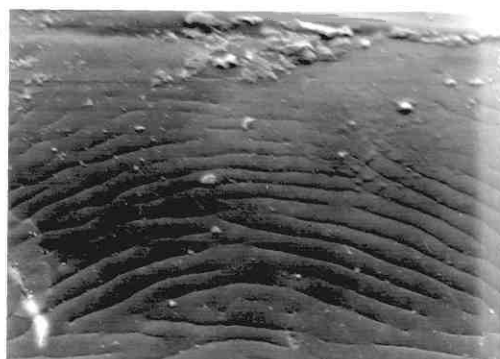
7.4



7.5



7.6



Plates 7.7 - 7.12. Scanning electron micrographs of Philonthus pronotum
microsculpture. (x 600).

7.7 P.cephalotes

7.8 P.nigriventris

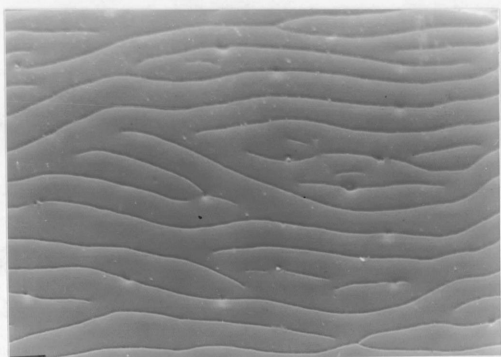
7.9 P.parcus

7.10 P.protenus

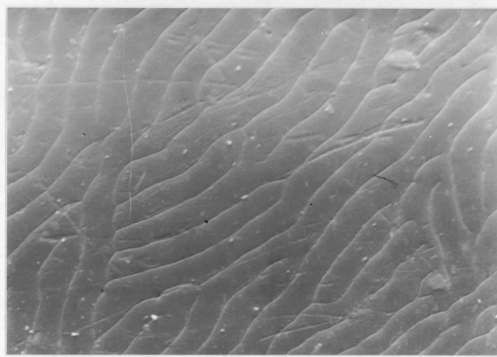
7.11 P.semiaenescens

7.12 P.sordidus

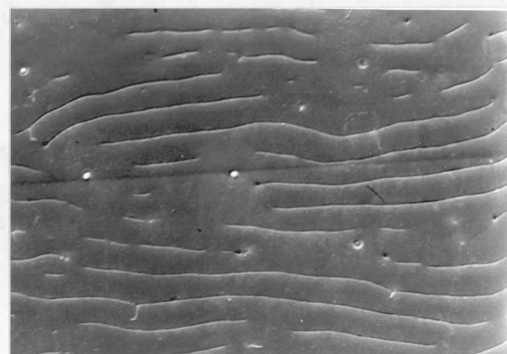
7.7



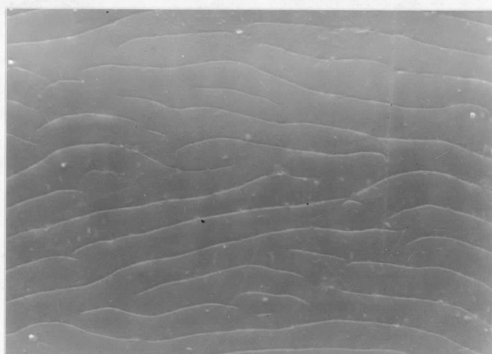
7.8



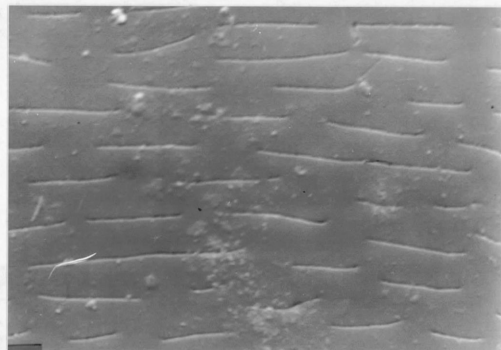
7.9



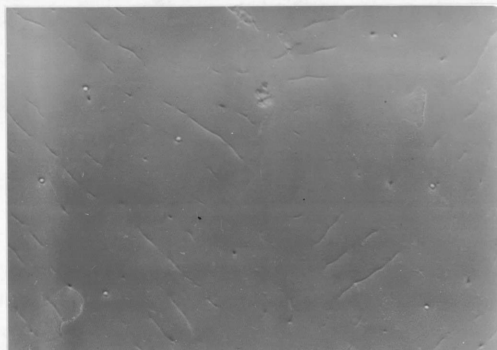
7.10



7.11



7.12



most common kind on the surface of the cuticle consists of a pattern of polygons 7-20 μm wide and frequently more or less hexagonal. Since this pattern occurs in the Thysanura and at least some part of the body of every pterygote insect examined, it seems that this is the primitive condition although it is often obliterated or replaced by very different types of microsculpture. Generally each polygon is secreted by a single epidermal cell; however, it was shown that in Philonthus marginatus each epidermal cell secreted 2-3 of the sculpture lines. Abdominal inter-segmental membranes, which are not subject to the same selection pressure as the cuticle, exhibit this type of sculpture (when it is present) in primitive staphylinids. This indicates that this is the primary condition, as opposed to sculpturation on more exposed parts of the cuticle which may exhibit an advantageous departure (Erwin, 1979).

Abdominal microsculpture in the group consists of transverse parallel lines with few branches, which are most often less widely spaced compared with the microsculpture of the head and pronotum.

7.2.2 Characters used to separate species in the P. sordidus-Group

Numerous characters, some more reliable than others, have been used by various authors to distinguish species in the group.

1. colour
2. shape, particularly of head and pronotum
3. metallic lustre of elytron
4. antennal-segment shape
5. extent of head microsculpture
6. extent of pronotal microsculpture
7. density of elytron puncturation
8. proximity of abdominal sculpture

9. genital characters

- a. form of median lobe apex
- b. form of lateral lobe
- c. distribution of lateral lobe peg setae
- d. ventral surface of lateral lobe with or without longitudinal ridge.

10. total body length

Characters 9 a. and c. are usually species-specific; 1, 3 and 10 are often not very reliable; 2 can only be satisfactorily used meristically; the remaining characters are multistate and are coded as in Section 7.2.3.1, and used here in an average linkage cluster analysis (simple matching coefficient) to provide a similarity dendrogram.

The form of the genitalia is species-specific and consequently frequently the most reliable characters for identification; these are figured (Figs. 7.2-7.6).

7.2.3 Numerical Taxonomy

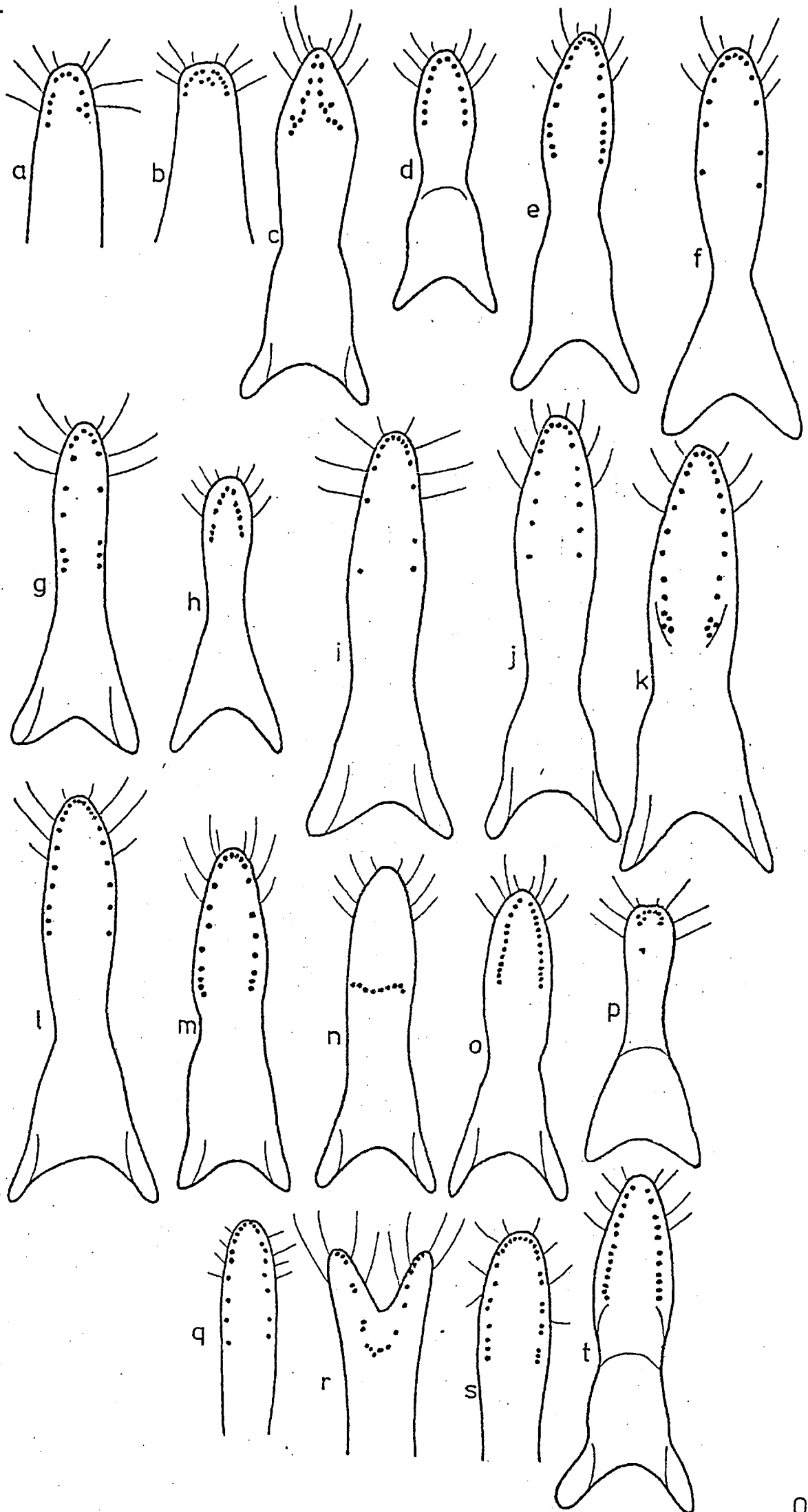
Numerical taxonomy according to Sokal & Sneath (1963) is "the numerical evaluation of the affinity or similarity between taxonomic units and the ordering of these units into taxa on the basis of their affinities".

The advantages of using a numerical method are that it is objective, repeatable because each step is known, and ensures full use of available data. It therefore enables a detailed analysis of quantitative or qualitative characters as well as operational taxonomic units (OTU's).

The disadvantages are apparent in the importance placed on overall resemblance since this does not necessarily indicate phylogenetic affinity, and there is a tendency to regard all characters

Fig.7.2. Male genitalia of the Philonthus sordidus-Group; lateral lobes,

- a) P.batkhezensis (after Coiffait,1974)
- b) P.bucharensis (after Coiffait,1974)
- c) P.cephalotes
- d) P.fletcheri
- e) P.friebe
- f) P.kashmiricus
- g) P.nigriventris
- h) P.noualhieri
- i) P.parcus
- j) P.protenus
- k) P.pseudoparcus.
- l) P.scribae
- m) P.sordidus
- n) P.sparsus
- o) P.spermophili
- p) P.subuliformis
- q) P.pentheri (after Coiffait,1974)
- r) P.potanini (after Coiffait,1974)
- s) P.sogdianus (after Coiffait,1974)
- t) P.microtophilus



0.2mm

Fig.7.3. Male genitalia of the Philonthus sordidus-Group; median lobes,
ventral view,

- a) P.batkhizensis (after Coiffait,1974)
- b) P.cephalotes
- c) P.fletcheri
- d) P.friebi
- e) P.kashmiricus
- f) P.microtophilus
- g) P.nigriventris
- h) P.noualhieri
- i) P.palmi
- j) P.parcus
- k) P.protemus

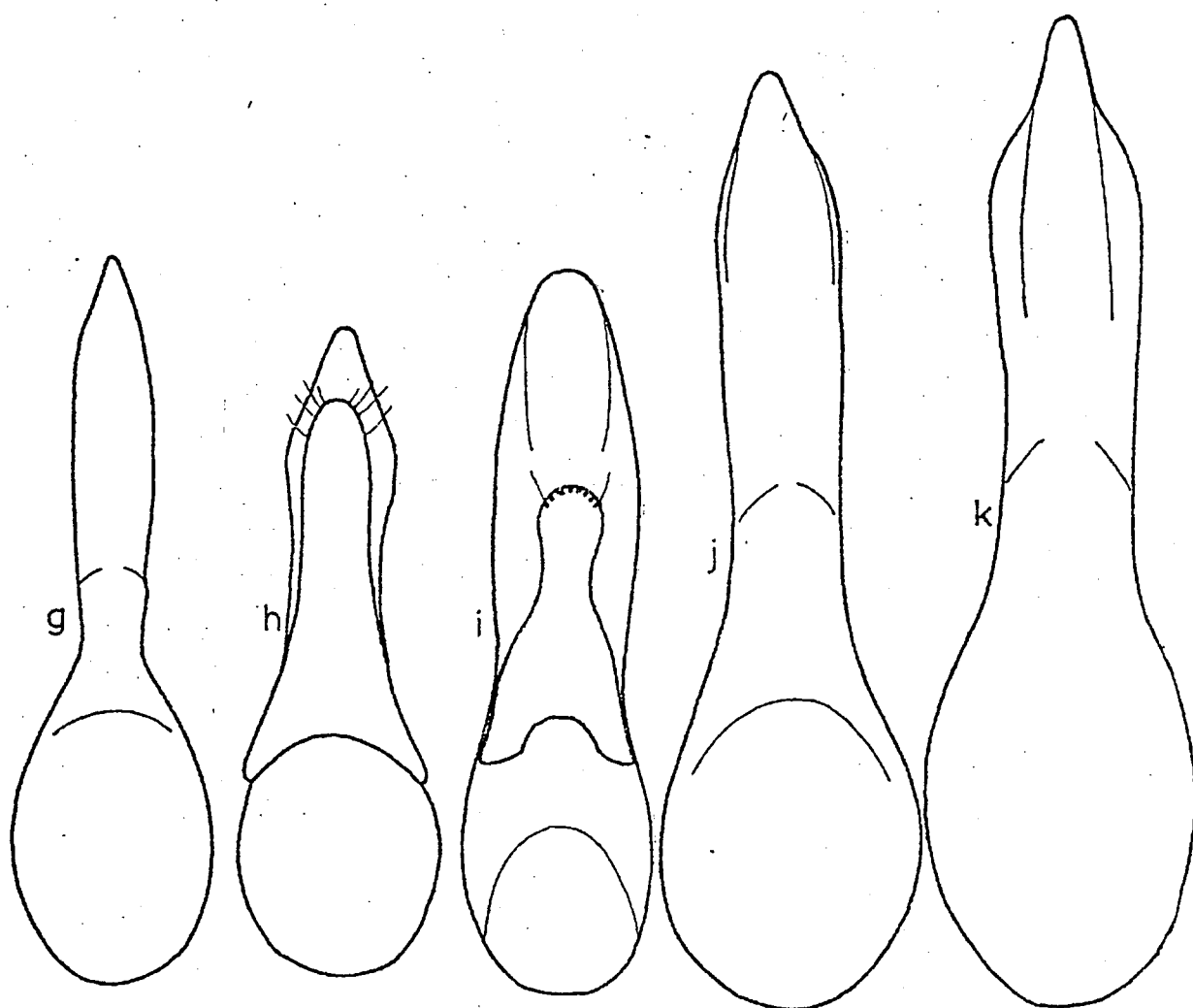
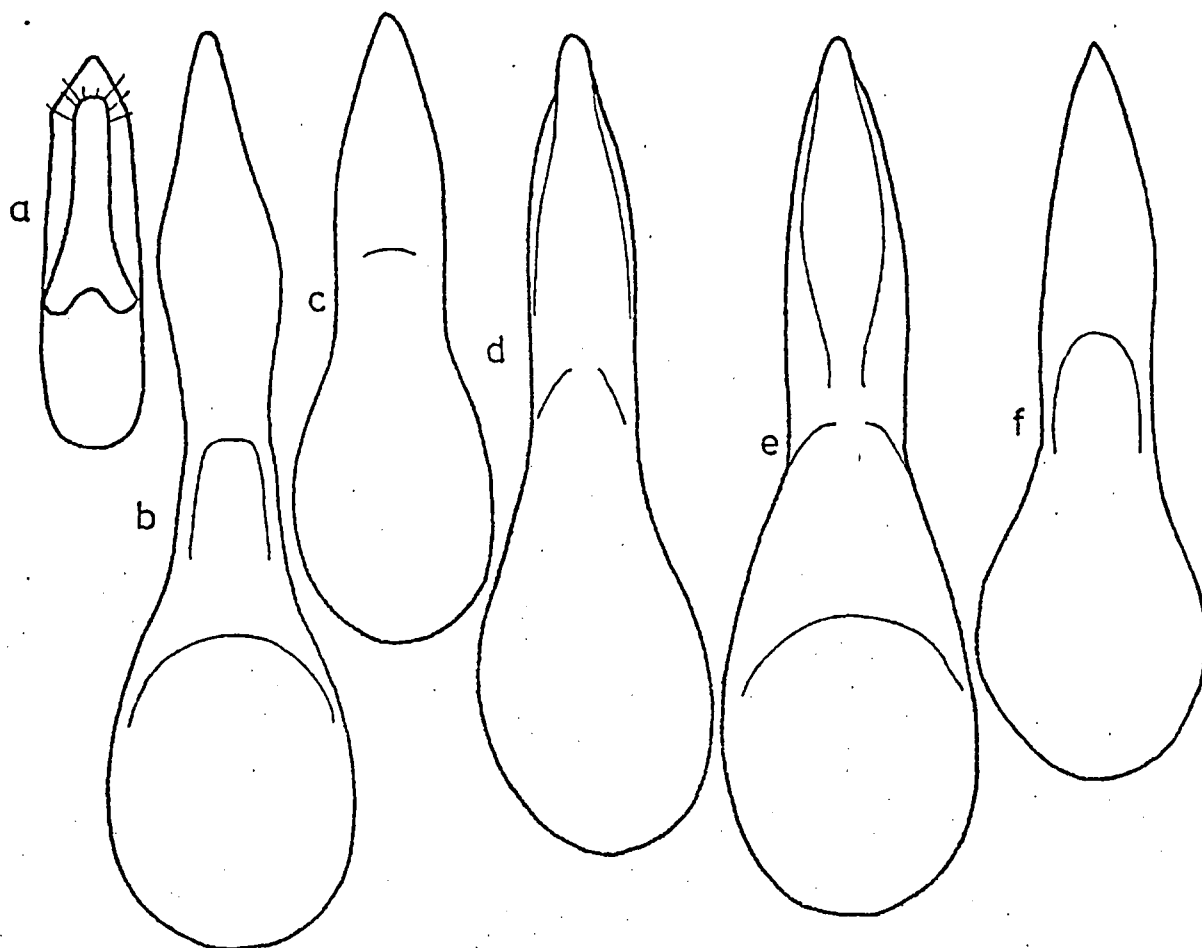
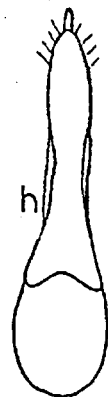
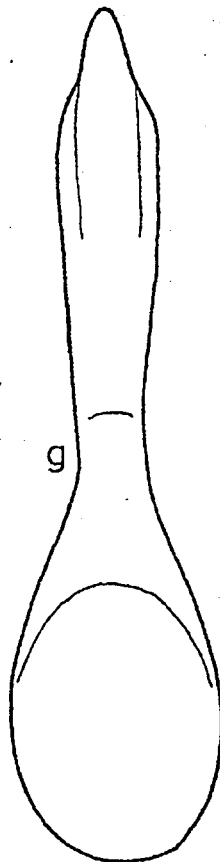
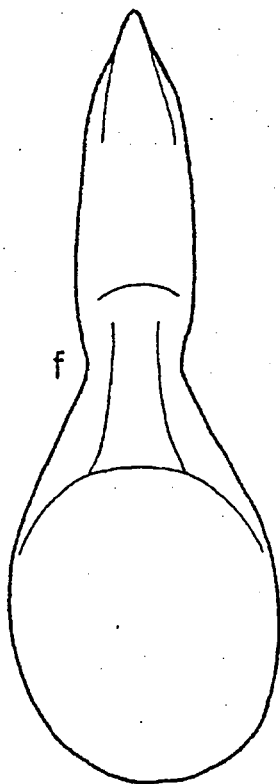
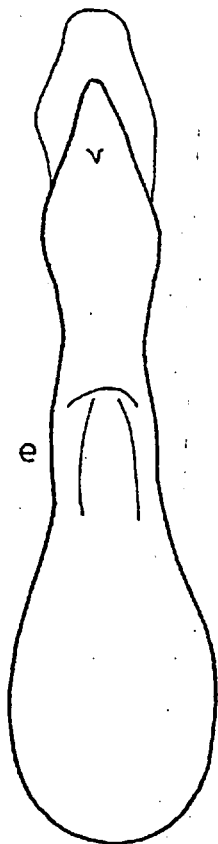
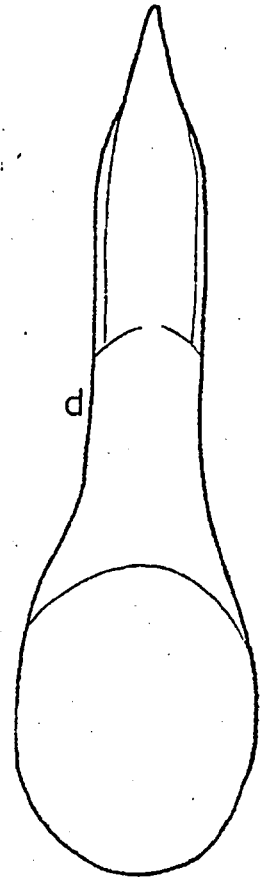
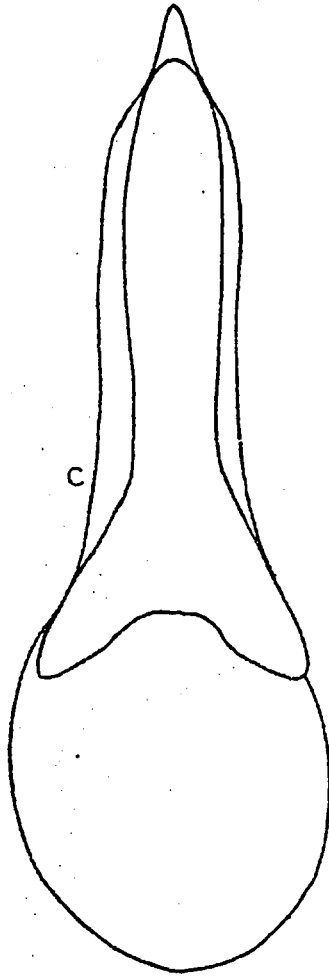
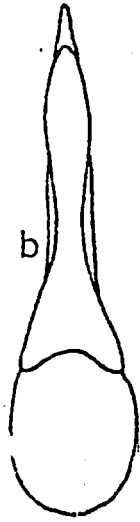
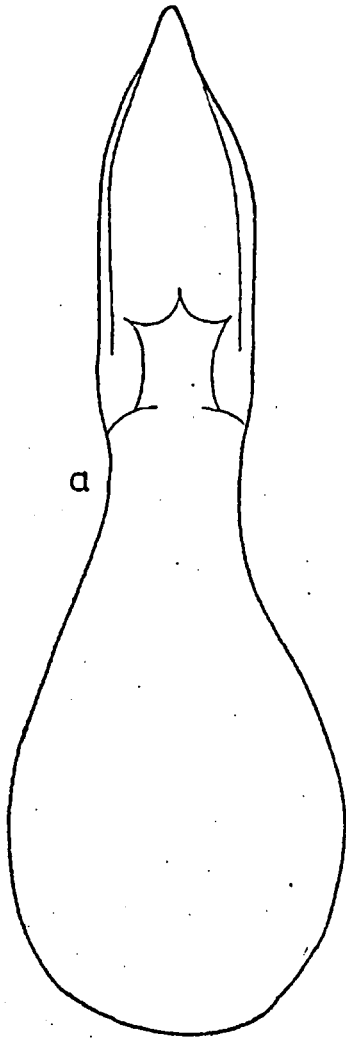


Fig.7.4. Male genitalia of the Philonthus sordidus-Group; median lobes, ventral view,

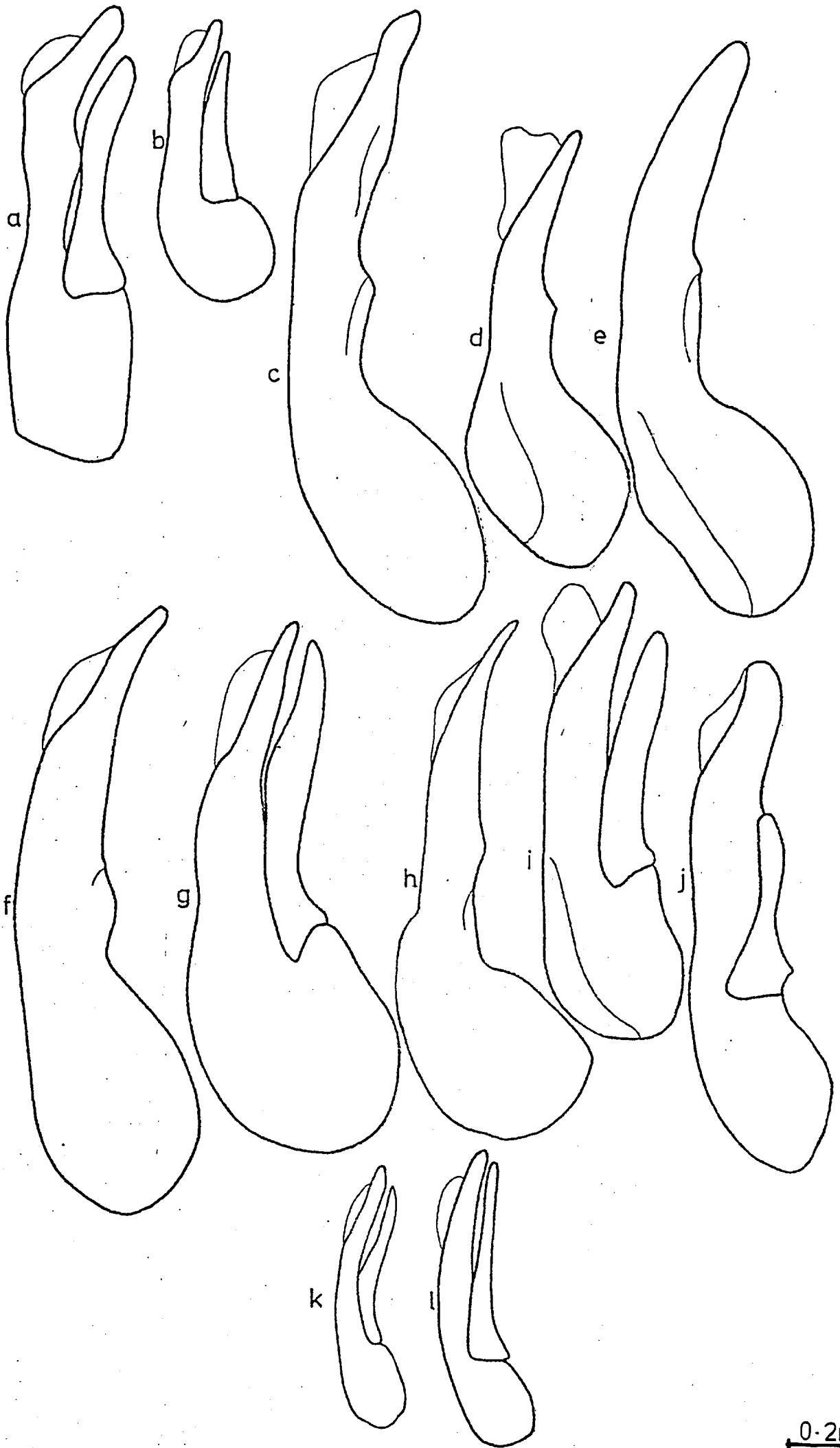
- a) P.pseudoparcus
- b) P.pholeophilus (after Coiffait,1974)
- c) P.scribae
- d) P.sordidus
- e) P.sparsus
- f) P.spermophili
- g) P.subuliformis
- h) P.pentheri (after Coiffait,1974)
- i) P.sogdianus (after Coiffait,1974)



0.2mm

Fig.7.5. Male genitalia of the Philonthus sordidus-Group; median lobes,
lateral view,

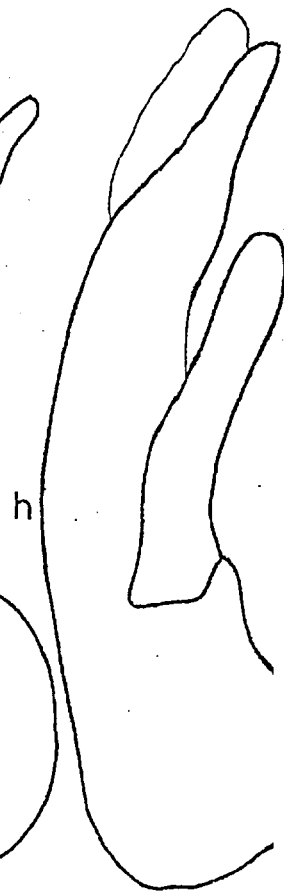
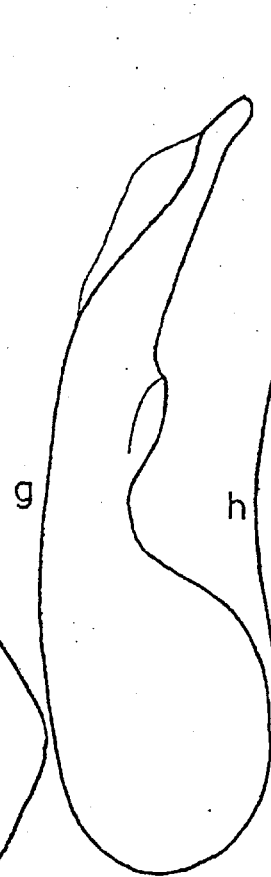
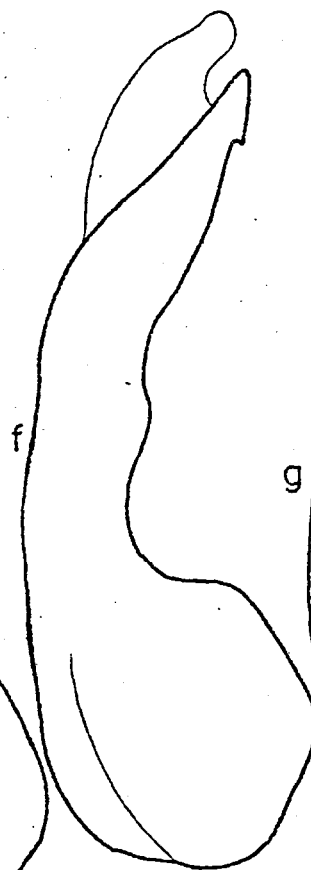
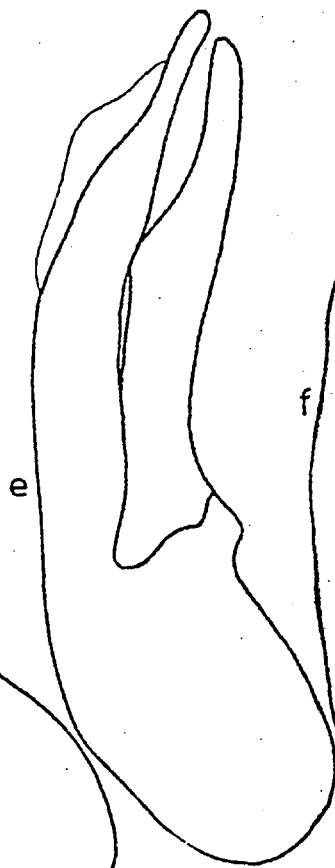
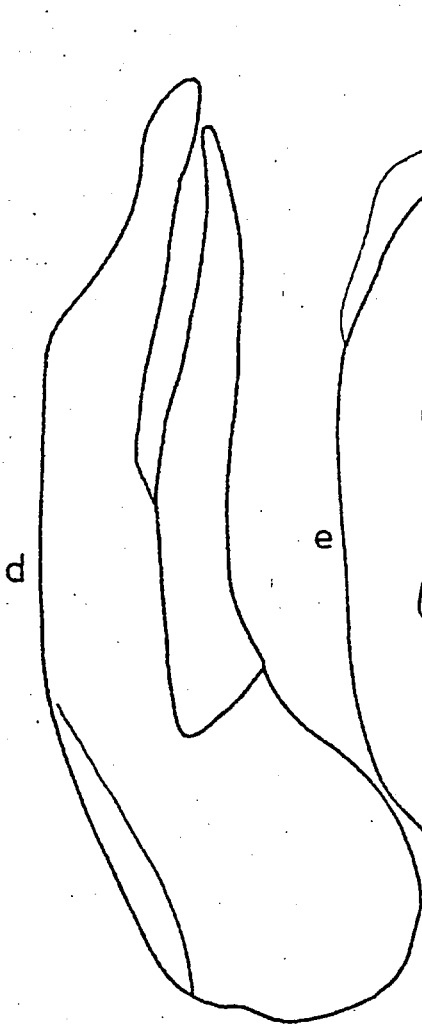
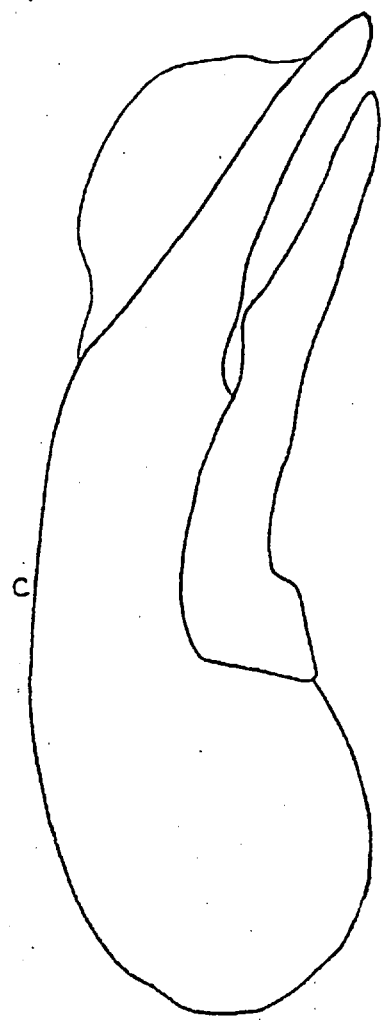
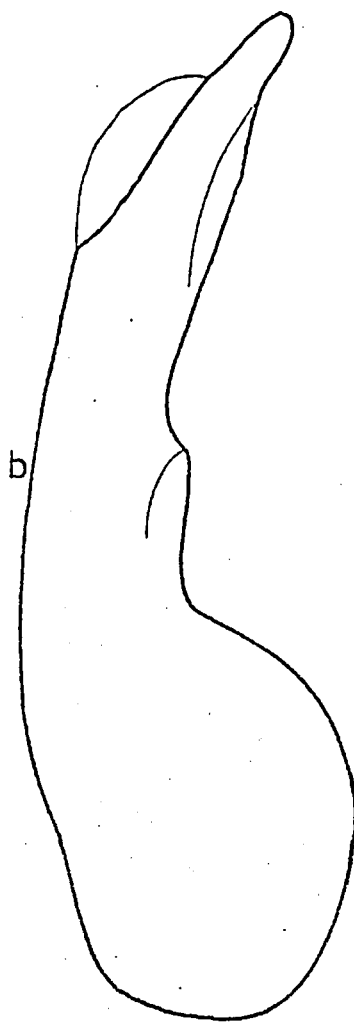
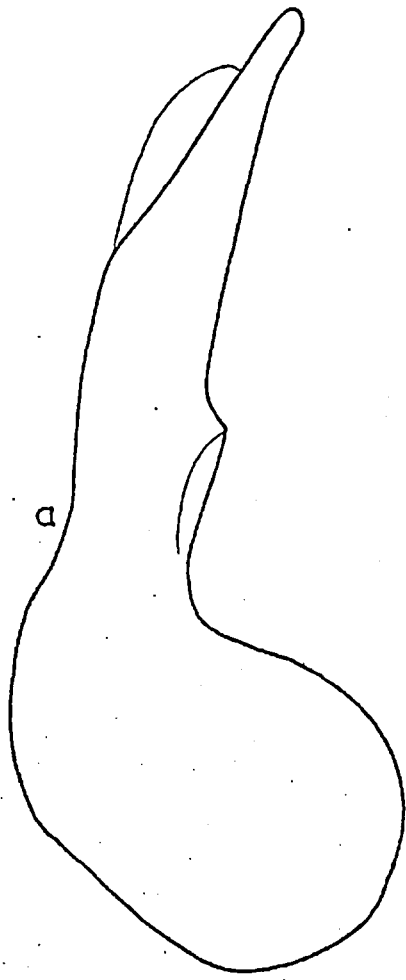
- a) P.batkhiensis
- b) P.bucharensis (after Coiffait,1974)
- c) P.cephalotes
- d) P.fletcheri
- e) P.friebi
- f) P.kashmiricus
- g) P.microtophilus
- h) P.nigriventris
- i) P.noualhieri
- j) P.palmi
- k) P.pentheri (after Coiffait,1974)
- l) P.sogdianus (after Coiffait,1974)



0.2mm

Fig.7.6. Male genitalia of the Philonthus sordidus-Group; median lobes,
lateral view,

- a) P.parcus
- b) P.protemus
- c) P.pseudoparcus
- d) P.scribae
- e) P.sordidus
- f) P.sparsus
- g) P.spermophili
- h) P.subuliformis



0.2mm

with equal weight which is an over simplification.

In this instance numerical methods are utilised to enable an analysis of a fairly large data matrix of characters of the P. sordidus-Group.

Since there is little relevant background information from out-group comparisons, which would indicate in which direction transformations in particular characters were leading in different groups, the aim here is to achieve a purely phenetic classification.

The programme used was an Average Linkage Cluster Analysis by J. C. Davis (1973) amended and extended by R. G. Davies, Zoology Department, Imperial College. The programme was adapted to use Gower Similarity Coefficients for qualitative characters.

In a cluster analysis taxa are arranged in a hierarchical manner in the form of a dendrogram which expresses the pattern of similarity coefficients, and clustering is based on overall resemblance.

In a single linkage cluster analysis a new OTU is added to a cluster if the similarity between it and any OTU already in the cluster falls below a certain level, i.e. the level of admission is gradually lowered by steps of equal magnitude. In complete linkage cluster analysis a new OTU is admitted to a cluster, only if it resembles all those already in the cluster. The average linkage cluster analysis takes the average of all the similarities in a cluster and admits a new OTU only if its similarity coefficient falls above a particular criterion level.

The Gower coefficient enables the use of mixed data, i.e. meristic and nominal, so that some characters may be ordered quantitatively and treated in terms of a distance relationship, while others are treated qualitatively. It is also possible to assign weights to certain characters if the information is available. In the case of the P. sordidus-Group all the characters are treated qualitatively

and assigned equal weights, to achieve a simple match/mismatch coefficient which results in a purely phenetic dendrogram.

7.2.3.1 Coding of Characters

24 species (OTU's) and 9 characters were used.

In 6 species there is missing data for four characters, and this is coded accordingly as -1 (Table 7.9).

Shape of Antennal segments 6-10 (A)

Quadrate	1
Slightly transverse	2
Transverse	3
Extremely transverse	4

Distribution of microsculpture on dorsal surface of head (HMD)

Uninterrupted, completely covering dorsal surface, (Plate 7.2)	1
Partially interrupted, completely covering dorsal surface	2
Interrupted, long and short lines covering dorsal surface (Plate 7.3)	3
Extremely interrupted, short lines covering dorsal surface (Plate 7.5)	4
Centre of dorsal surface devoid of microsculpture (Plate 7.4)	5
Entirely devoid of microsculpture	6

/Proximity of head microsculpture (HMP)

No microsculpture	0
Close (Plate 7.6)	1
Intermediate, (e.g. <i>P. nigriventris</i>) (Plate 7.2)	2
Distant (Plate 7.3)	3

Distribution of microsculpture on dorsal surface of pronotum (PMD)

Uninterrupted, completely covering dorsal surface (Plate 7.8)	1
Partially interrupted, completely covering dorsal surface	2
Interrupted, long and short lines covering dorsal surface (Plate 7.10)	3

/Footnote: "Proximity" is used to indicate the closeness of the parallel lines of sculpture.

TABLE 7.9

. Coding of Characters for Numerical Analysis of the Philonthus sordidus Group

Shape of antennal segments 6-10	1	3	4	4	1	1	3	3	3	1	3	4	3	3	3	3	1	2	2	1	1	3	3
Distribution of head microsculpture	3	3	1	1	1	1	1	1	1	6	1	1	1	3	5	3	3	1	5	3	6	5	1
Proximity of head microsculpture	3	-1	2	-1	2	-1	1	2	3	0	2	2	-1	2	-1	2	1	-1	1	3	0	1	2
Distribution of pronotum microsculpture	5	3	2	1	1	3	2	1	3	6	1	1	1	5	5	3	3	1	6	5	6	6	1
Proximity of pronotum microsculpture	2	-1	1	-1	1	-1	1	2	3	0	2	2	-1	1	-1	1	2	-1	0	2	0	0	2
Proximity of abdomen microsculpture	1	-1	2	-1	1	2	4	1	2	1	5	3	-1	1	-1	1	4	-1	1	1	2	1	1
Density & depth of elytral punctures	1	6	6	6	4	1	6	6	1	6	6	3	4	4	6	4	1	5	1	1	1	6	5
Presence of longitudinal ridge on lateral lobe	2	-1	1	-1	2	-1	1	1	2	1	2	2	-1	1	-1	1	2	-1	2	1	2	1	2
Total body length	2	3	2	3	3	3	1	2	3	2	2	1	3	3	2	3	3	2	3	2	2	1	2
	agyrtes	baicalensis	batkhizensis	bucharensis	cephalotes	eidmanni	fletcheri	friebe	kashmiricus	microtophilus	nigriventris	noualhierii	palmi	parcus	pholeophilus	protemus	pseudoparcus	psyllophagus	scribae	sordidus	sparsus	spermophilii	subuliformis

Extremely interrupted, short lines covering dorsal surface (Plate 7.11)	4
Centre of dorsal surface devoid of microsculpture (Plate 7.12)	5
Entirely devoid of microsculpture	6

/Proximity of pronotal microsculpture (PMP)

No microsculpture	0
Close (Plates 7.7 & 7.9)	1
Intermediate (e.g. <u>P. nigriventris</u>) (Plate 7.8)	2
Distant	3

/Proximity of abdominal microsculpture related to P. sordidus (AMP)

1 = <u>P. sordidus</u>	1
x 2	2
x $1\frac{1}{2}$	3
x $\frac{3}{4}$	4
x $\frac{1}{2}$	5

Density and depth of Elytral puncturation (E)

Sparse + fine	1	Sparse + deep	2
Medium + fine	3	Medium + deep	4
Dense + fine	5	Dense + deep	6

Presence of longitudinal ridge on ventral surface of lateral lobe (LL)

Present	1
Absent	2

Total Body Length (S)

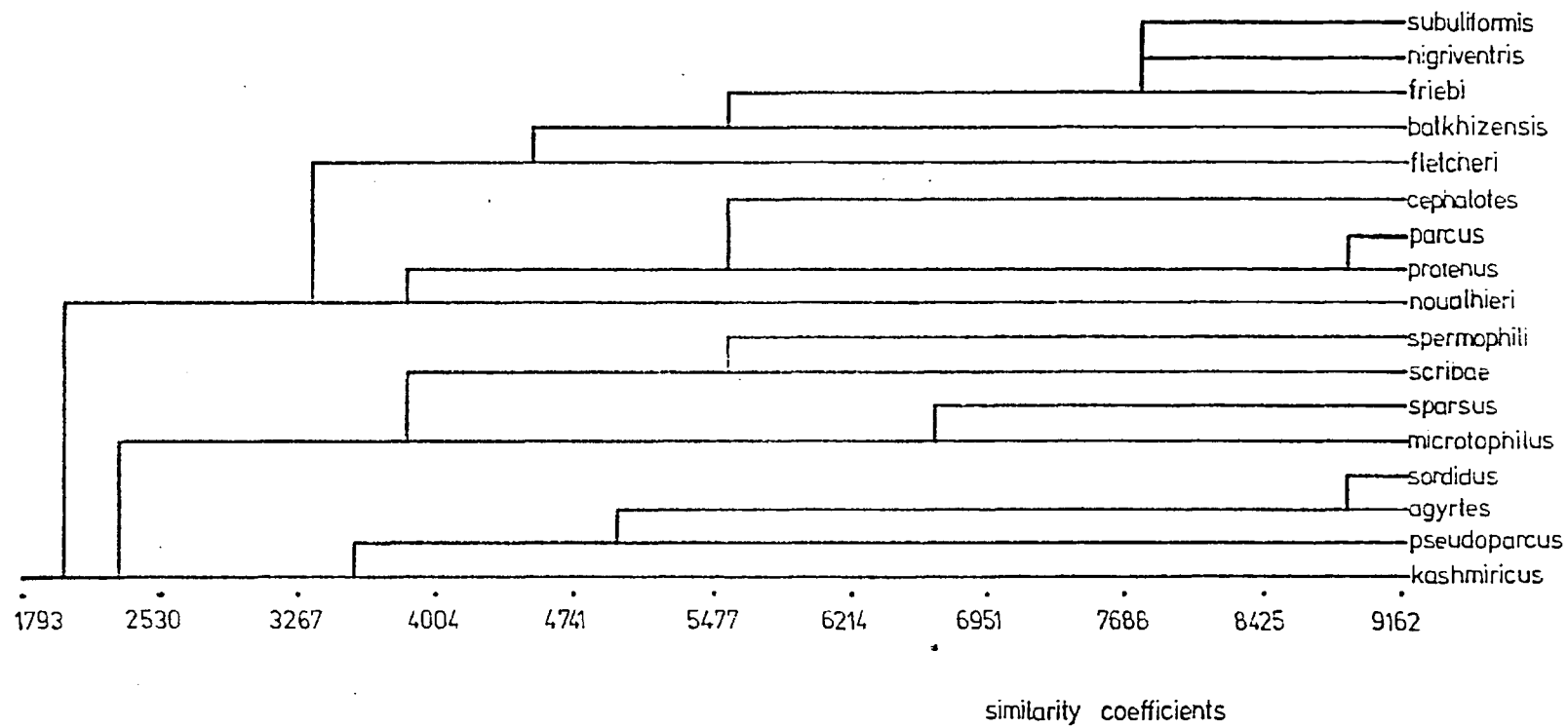
5 - 6 mm	1
- 7 mm	2
- 8 mm	3

The coding of characters is done on a nominal scale, the ordering bears no significance.

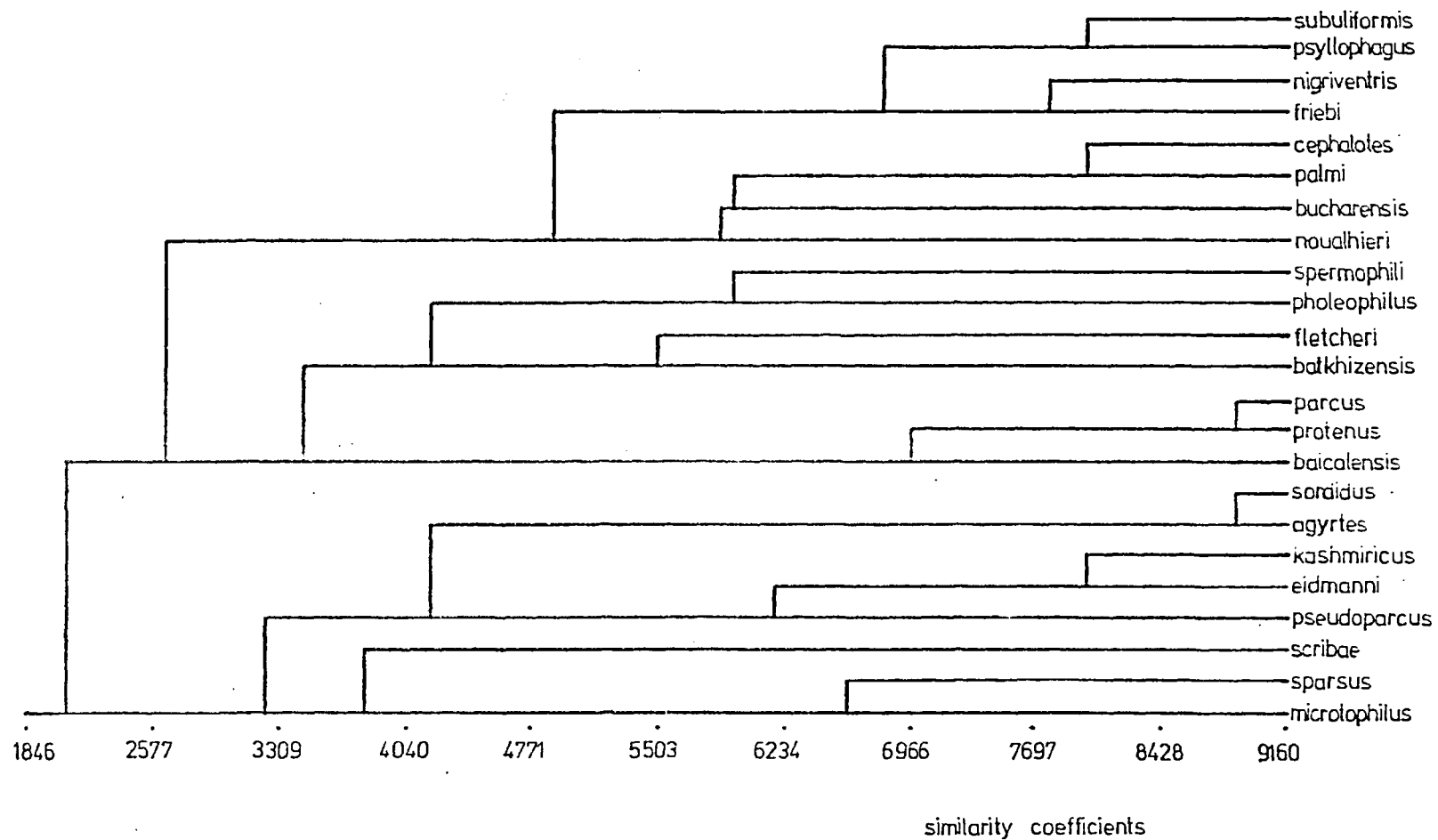
Phenogram 7.1

17 species with data for 9 characters.

Phenogram 7.1 17 species of Philonthus using data for 9 characters.



Phenogram 7.2 24 species of Philonthus, 17 with data for 9 characters and 6 with data for 5 characters.



Phenogram 7.2

24 species; 17 with data for 9 characters, 6 with data for 5 characters.

Although data is incomplete in Phenogram 7.2, it provides an indication of where the remaining 6 species may be placed.

7.2.3.2 Results of Numerical Taxonomy

The decision to use only nine characters must limit the importance placed on the positioning of species in the group. Clearly so few characters are insufficient for use in establishing phylogenetic relationships.

The characters used by various authors to separate the species have been identified. Because of the uniform nature of the group these characters are few in number; those which appear to be the most significant have been utilised in the present analysis. Although it is more usual to use all the available characters some are less easy to define, e.g. colour, while others are subject to intraspecific variation, illustrated in the studies on Quedius mesomelinus (Section 6) and may require a meristic approach which is not attempted here. A numerical analysis which produces a phenetic classification overlooks the occurrence of evolutionary convergence in certain characters which can only be ascertained by a broad knowledge of the genus as a whole. Such characters include shape of different parts of the body, which may be a consequence of living in a particular type of habitat and is responsible for common features in otherwise unrelated species. Information of this kind can be incorporated into a numerical analysis if allowance is made during character coding. Coding may also be adapted to include ordering, weighting, and euclidean distance in the analysis when the appropriate information is available.

The results are presented as phenograms. Phenogram 7.1 is

TABLE 7.10

Common characters within groups of species in Phenogram 7.1

	A	HMD	HMP	PMD	PMP	AMP	E	LL	S
1. <u>P. subuliformis</u>									
<u>P. nigriventris</u>	3,4	1	1,2	1,2	1,2	1,2,4,5	5,6	1,2	1,2
<u>P. friebi</u>									
<u>P. batkhizensis</u>									
<u>P. fletcheri</u>									
<u>P. cephalotes</u>									
<u>P. parvus</u>									
<u>P. protenus</u>	1,3,4	1,3	2	1,3,5	1,2	1,3	3,4	1,2	2,3
<u>P. noualhieri</u>									
2. <u>P. spermophili</u>									
<u>P. scribae</u>	1,2,3	5,6	0,1	6	0	1,2	1,6	1,2	1,2,3
<u>P. sparsus</u>									
<u>P. microtophilus</u>									
<u>P. sordidus</u>									
<u>P. agyrtes</u>									
<u>P. pseudoparcus</u>	1,3	1,3	1,3	3,5	2,3	1,2,4	1	1,2	2,3
<u>P. kashmiricus</u>									

TABLE 7.11

Common characters within groups of species in Phenogram 7.2

	A	HMD	HMP	PMD	PMP	AMP	E	LL	S
1. <u>P. subuliformis</u>									
<u>P. psyllophagus</u>									
<u>P. nigriventris</u>	1,3	1	2	1	2	1,5	5,6	1,2	2
<u>P. friebi</u>									
<u>P. cephalotes</u>									
<u>P. palmi</u>	1,3,4	1	2	1	1,2	1,3	3,4,6	2	1,3
<u>P. bucharensis</u>									
<u>P. noualhieri</u>									
<u>P. spermophili</u>									
<u>P. pholeophilus</u>	3,4	1,3,5	1,2	2,3,5,6	0,1	1,2,4	4,6	1,2	1,2,3
<u>P. fletcheri</u>									
<u>P. batkhizensis</u>									
<u>P. parvus</u>									
<u>P. protenus</u>									
<u>P. baicalensis</u>									

TABLE 7.11 (Continued)

	A	HMD	HMP	PMD	PMP	AMP	E	LL	S
2. <u>P. sordidus</u>									
<u>P. agyrtes</u>	1,3	1,3	1,3	3,5	2,3	1,2,4	1	1,2	2,3
<u>P. kashmiricus</u>									
<u>P. eidmanni</u>									
<u>P. pseudoparcus</u>									
<u>P. scribae</u>									
<u>P. sparsus</u>									
<u>P. microtophilus</u>	1,2	5,6	1,0	6	0	1,2	1,6	1,2	2,3

based on complete data for 17 species. While it must be remembered that linkages at the top of the dendrogram are more reliable than those at the base, there is an apparent division of the species into two groups, each of these in turn divided into two subgroups; Table 7.10, Phenogram 7.1. The characters represented by each group are listed and it will be noted that the groups are not definitive.

Phenogram 7.2 includes all the information from Phenogram 7.1 with six additional species in which data is available for only 5/9 characters. Phenogram 7.2 attempts to place these remaining species in their approximate positions in the classifications; Table 7.11, Phenogram 7.2.

The difference between the two phenograms can be explained to some extent by the unavoidable additional weight placed on the 5/9 characters which are present for all the species. It is notable that while the division into two groups remains, P. spermophili is transferred from group 2 to group 1 in the second phenogram on the basis of one character alone, (the transverse antennal segments).

Although a classification of this type is unlikely to be directly indicative of phylogenetic relationships, the more obvious groupings may be used as a basis for further investigations to look for synapomorphic characters, sister-species and natural groupings. It is suggested that the following groups and species pairs should be initially considered in this way:

P. subuliformis
 (P. nigriventris
 (P. friebi

P. cephalotes
 (P. palmi

- P. parvus
- (P. protenus
- (P. baicalensis

- P. sordidus
- (P. agyrtes

- P. kashmiricus
- (P. eidmanni
- (P. pseudoparcus

- P. sparsus
- (P. microtophilus

7.2.4. Suggestions Regarding Possible Relationships within the P. sordidus-Group

Taking into account the results of the numerical analysis and detailed morphological comparison of the species, with a consideration of additional characters, including the form of the genitalia, the following species are considered as being closely allied. (Refer to Table 7.9).

1. P. subuliformis and P. friebi
 - a. general body form
 - b. colouration
 - c. head with markedly squared posterior angles
2. P. batkhizensis and P. noualhieri
 - a. head with markedly squared posterior angles similar to P. subuliformis to which they may be close.
 - b. weak but dense elytral sculpture, also in P. subuliformis
 - c. antennal segments 6-10 very transverse.
 - d. head microsculpture markedly longitudinal in the centre of the dorsal surface.
 - e. form of the median lobe (Fig. 7.3h, 7.5a, & 7.5i)
 - f. short, almost truncate lateral lobe (Fig. 7.2a & 7.2h).

Items c., d., and f., are also characteristic of P. bucharensis (Coiffait, 1967) which, although it has not been examined in the present investigation, may well be near to P. batkhizensis and P. noualhieri.

3. P. protenus and P. parvus

Striking similarity in all characters, differing only in the distribution of pronotal microsculpture.

4. P. sordidus and P. agyrtes

Refer to previous note (Section 7.2) suggesting that P. agyrtes may be an aberrant form of P. sordidus.

5. P. cephalotes and P. palmi

Refer to previous note (Section 7.2) suggesting that P. palmi may be an aberrant form of P. cephalotes.

6. P. macies and P. eidmanni

If P. macies is to be considered part of the group, there are similarities in the type of pronotal microsculpture with P. eidmanni.

7. Most of the species with red elytra may be near to each other; these include P. plagiatus and some other species which may or may not be part of the group, many of them are also ground nest dwelling species;

<u>P. batkhizensis</u>	already discussed
<u>P. eidmanni</u>	?
<u>P. noualhieri</u>	already discussed
<u>P. pentheri</u>	nest dwelling
<u>P. pholeophilus</u>	nest dwelling
<u>P. plagiatus</u>	?
<u>P. propinquus</u>	?
<u>P. psyllophagus</u>	nest dwelling
<u>P. scribae</u>	nest dwelling
<u>P. sogdianus</u>	?

P. eidmanni, P. pentheri, P. pholeophilus, P. plagiatus and P. scribae also share a similar form of genitalia where the lateral

lobe is more markedly waisted halfway along its length than other species in the group. Coiffait (1974) suggests that P. pentheri and P. propinquus, neither of which were examined in the present study, are probably closely related.

7.2.5 Possible Relationships of Species excluded from the P. sordidus-Group

A number of the species considered by certain authors to be part of the P. sordidus-Group, but which have been excluded here, bear a distinct similarity to each other and are likely to be closely related, i.e. P. alaiensis, P. diversus, P. scoticus, P. semiaenescens and P. siegwaldi.

The similarities are:

1. The inter-ocular punctures are equidistant, or the centre pair are considerably closer together.
2. The head and pronotal microsculpture is of a characteristic type not found in the P. sordidus-Group as it is defined here, considerably interrupted into short lines (Plates 7.5 & 7.11).
3. The lines of the abdominal sculpture are very close.
4. The median lobe is broad and flattened; triangular at the apex.
5. The lateral lobe is bifid and situated dorsally on the median lobe at rest in the abdomen.

P. diversipennis also shares these characteristics but differs in the distribution of the head and pronotal microsculpture, where the centre of the dorsal surface is devoid of sculpture, and the lines of the abdominal sculpture are widely spaced.

P. fimetarius exhibits the same characteristic microsculpture as the P. alaiensis-Group and has a broad median lobe although this is rounded at its apex. The lateral lobe is of different structure and, while not strictly bifid, is indented in the mid line. The

genitalia are situated at 90° in the abdomen at rest. The inter-ocular punctures are not equidistant, the central pair are widely spaced.

The investigation began with an inquiry into the relationship of P. sordidus with P. cephalotes. It must be concluded that while they are without doubt fairly closely related to each other, the closeness of their relationship cannot be predicted with any great confidence. They are unlikely to prove to be sister-species.

SECTION 8

DISCUSSION.

The role of secondary sexual features which are thought to operate in species specific tactile recognition signalling has been investigated in male Staphylinidae. Signals of this type are exchanged at close quarters once the potential mating pair have "made contact". The composition of these features is in distinct contrast to other secondary sexual features in the Staphylinidae and other families which are known to fulfil different functions.

A signal system of the type referred to above is typical of species which are predominantly found in particular ecological situations. For example, heterogeneous substrate zone habitats, where resources are patchily distributed support closely related pairs or groups of species which coexist apparently breaking Gause's rule of competitive exclusion. Synanthropic habitats such as compost or vegetable refuse heaps are an example of this particular ecological situation and have been used as a basis for the study of the two main species in the present thesis. Morphological comparisons of sympatric and allopatric species pairs show that divergence in the signal system is a frequent occurrence in the former and this may provide evidence for their operation as part of a recognition system.

The distribution of records of cross matings and hybridisation through the Coleoptera highlight the differences in the types of pre and post-mating reproductive barriers utilised by species in different ecological situations. Groups in which closely related species are separated by pre-mating barriers of the "mate avoidance" type i.e. they are separated by seasonal, and other temporal or ecological factors, are commonly recorded in the literature owing to

the frequent breakdown of such barriers, occurring often under artificial experimental conditions. Although cross matings may occur, post mating barriers are operative in some and hybrids have reduced viability. In groups where species are sympatric and exchange specific signals at close quarters, records of cross matings and hybridisation are absent. This indicates that specific signal systems are likely to operate as pre-mating reproductive barriers and their development and divergence may be directly concerned with speciation. In a situation where there is more than one optimal genotype in a population these will be selected for while less favoured genotypes will be selected against. Thus, in the face of gene flow, selection for assortative mating and consequential hybrid disadvantage will be responsible for the gradual development of reproductive barriers between diverging populations.

Emphasis has been placed on the mode of operation of one particular signalling system thought to be involved in the exchange of specific tactile recognition signals, i.e. the patterns of peg setae which occur on the lateral lobes of the male genitalia of some Staphylinini. Information gained from studies on mating behaviour and ultrastructure seem to confirm the hypothesis that peg setae are probably redundant mechanoreceptors pre-adapted for development into a specific tactile signalling system to be used at close quarters during mating. Different behavioural responses, both intra and interspecific, were examined in Philonthus species, in order to understand the operation of such a reproductive barrier and indicate that courtship comprises a battery of signals and stimuli required to coax a coy female to be receptive. In closely related species, however, divergence of signal seems only to occur in one system, the patterns of peg setae used as a final signal in the sequence. Differences in courtship behaviour as a whole are minute although these may indeed

be significant. Contact chemoreception is thought to be operative but the specificity of this remains unknown.

The variability in putative tactile recognition features compared with other external features is generally limited. This is illustrated by Quedius mesomelinus and Q. maurus, where, beyond the area of overlap of the two species, Q. mesomelinus exhibits much greater variation in such features with several distinct populations apparently in the process of divergence. Such inter-population variability, where Q. maurus is not present, is an indication of the importance of the secondary sexual features in specific mate recognition within the area of overlap. A preliminary analysis of peg patterns illustrates their intraspecific stability and interspecific divergence, and clines in genital characters cannot be directly correlated with those in other external features, indicating that environmental factors which may well affect the variability of the latter are not likely to be involved in that of the former. When considering the development of reproductive barriers between supposed sister species it is important to assess their precise relationship. A preliminary phylogenetic examination of the two main species involved in the present work, along with other members of the group of species to which they belong, indicates that they are undoubtedly very closely related but are probably not sister species. Nevertheless, in the Philonthus sordidus-Group the majority of the members possess peg patterns similar to that of P. sordidus, and that of P. cephalotes represents a divergence which is likely to be connected with their close ecological association. A study of this type necessitates pursuit of a number of different aspects, e.g. morphology, taxonomy, phylogeny, behaviour, and inevitably only limited time can be spent in each area. There is much scope for development of this work by following up some lines

already pursued and proceeding to new areas. The histology of peg setae and their examination by Transmission Electron Microscopy to clarify their structure and function needs more attention perhaps with a comparison of those from different sites, e.g. abdomen, legs and genitalia, and in different groups, perhaps in those where peg setae are thought to be a recent acquisition. The possibility of using a numerical analysis of peg patterns should be investigated in order to determine the limits of variability and assess the differences between closely related sympatric species particularly in cases where pattern differences are more subtle than between Philonthus sordidus and P. cephalotes. Phylogenetic relationships within the Philonthus sordidus-Group require clarification in the light of broader knowledge of the Philonthini as a whole.

Biochemical analysis for the detection and determination of the female chemical perceived by a male upon contact may be achieved by gas-liquid chromatography. Subsequently its specificity could be tested. Studies which involve making models of female bodies with various parts of a live female attached, to locate the source and time of chemical production are unlikely to be successful in species like Philonthus where the occurrence of mating behaviour cannot be relied upon under experimental conditions.

Ecological studies are required to determine the precise extent of the proximity of mature adults of sympatric species in fragmented habitats of the type discussed above, as well as the temporal and spatial relationships of the species in the field. It would be interesting to pursue the Quedius work in Europe to assess the state of isolation of the "varieties" of Q. mesomelinus and to collect more thoroughly for transitional forms.

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Appendix 1.

List of species in which cross mating and hybridisation
has occurred

Key to Symbols

- ↑ reciprocal crossing
e under experimental conditions
n in field conditions
cm cross mating
h hybrid produced
* parapatric species

CARABIDAEPuisségur (1962a,
1964)Carabus auronitens subfestivus Oberthur ♂C. punctatoauratus barthei Lapo. ♀ h,e

Raynaud (1968a)

C. auronitens subfestivus Oberthur ↑
C. lateralis

h,e

Raynaud (1968b)

C. auronitens festinus Dej. ♂C. solieri Dej. ♀ h,e

Puisségur (1962b)

C. auronitens festinus Dej. ♂C. splendens Ol. ♀ h,ePuisségur (1960)
Lequet (1973)C. auronitens festinus Dej. ♂C. hispanus F. ♀ h,e"
Puissegur (1959b)
Sturani (1961)

cm,e

C. auronitens F. ♂C. splendens Ol. ♀ h,e

Fradois (1943)

C. auronitens armoricanus Oberth. ♂C. auronitens var. putzeysi Mors. ♀ * h,e

Leleup (1938)

C. auronitens F.C. cupreonitens Kraatz h,n

Cousin (1947)

C. auronitens festinus Dej.C. splendens ammonius Lap. h,n

Raynaud (1970)

C. auronitens festinus Dej.C. hispanus latissimus Lap. h,n

"

C. auronitens F.C. lateralis Chevrolat h,n

"

<u>C. arvensis</u> Herbst	h,n	Mandl (1954)
<u>C. ullrichi</u> Costa		
<u>C. arvensis</u> Herbst	h,n	"
<u>C. cancellatus</u> Ill.		
<u>C. depressus</u> Ban.	h,n	"
<u>C. fabricii</u> Panz.		
<u>C. glabratus</u> Payk.	h,e	Roubal (1924)
<u>C. obsoletus</u> Sturm		
<u>C. depressus</u> Bon. (♀ <u>depressus lucens</u>)	h,n	Sturani (1961)
<u>C. cychroides</u> Baudi (♂)	(cm,e)	"
<u>C. depressus</u> Bon.	h,n	"
<u>C. irregularis</u> F.		Jorger (1925)
<u>C. monilis</u> F.	h,n	Kolbe (1913)
<u>C. purpurascens</u> F.		
<u>C. monilis</u> F.		
<u>C. cancellatus</u> Ill.	h,n	"
<u>C. monilis</u> F. ♂	h,e	Mellerio (1918)
<u>C. violaceus</u> L. ♀		
<u>C. monilis</u> F. ♂	h,e	"
<u>C. auratus</u> ♀		
<u>C. hispanus</u> F.	h,e	Puisségur (1960)
<u>C. rutilans</u> Dej. ↑		
<u>C. hispanus</u> F. ♀	h,e	"
<u>C. splendens</u> Ol. ♂	h,e	2. Puisségur & Bonadona (1973)
<u>C. hispanus</u> F. ♂	h,e	Puisségur (1960)
<u>C. lineatus</u> Dej. ♀		
<u>C. purpurescens</u> F.	h,n	Cleu (1968, a & b)
<u>C. violaceus</u> L.		
<u>C. punctatoauratus</u>	h,n	Nicolas (1923)
<u>C. splendens</u> Ol.		
<u>C. punctatoauratus pseudofestivus</u>		
Barthe ♂	h,e	Puisségur (1960)
<u>C. splendens</u> Ol.		
<u>C. punctatoauratus pandellei</u>		
<u>aurocostatus</u> Dej.	h,n	Raynaud (1970)
<u>C. splendens</u> Ol.		
<u>C. punctatoauratus boscensis</u>		
Nicolas	h,n	" , Lequet (1973)
<u>C. splendens</u> Ol.		

<u>C. punctatoauratus pandellei</u> Géhin	h,n	Raynard (1970)
<u>C. splendens</u> Ol.		
<u>C. punctatoauratus boscensis</u> pseudofestivus Lap.	h,n	"
<u>C. splendens</u> Ol.		
<u>C. punctatoauratus barthei</u> Lap.	h,n	" ,Lequet (1973)
<u>C. splendens</u> Ol.		
<u>C. punctatoauratus farinesi</u> Dej.	h,n	"
<u>C. splendens</u> Ol.		
<u>C. splendens lapurdanus</u> Lap.	h,n	"
<u>C. lineatus troberti ursuius</u> Lap.		
<u>C. splendens</u> Ol. 2. ♀	h,n	" ,Lequet (1973)
<u>C. lineatus</u> Dej. ♂	2. h,e	,Puisegur (1960)
<u>C. splendens lapurdanus pallens</u> Lap.	h,n	"
<u>C. lineatus basilicus</u> Chevrolat		
<u>C. splendens ammonius</u> Lap. 2.	h,n	" ,Raynaud (1968b)
<u>C. lateralis</u> Chevr. = <u>lineatus</u> Dej. ↑	2. h,e	
<u>C. splendens</u> Ol.	h,n	Bruneau de Miré (1964)
<u>C. rutilans opulentus</u> Oberthur		
<u>C. splendens</u> Ol. ↑	cm,e	Sturani (1961)
<u>C. intricatus</u> L.		
<u>C. splendens</u> Ol. ♀	cm,e	"
<u>C. olympiae</u> Sella ♂		
<u>C. splendens</u> Ol. ♀	cm,e	"
<u>C. granulatus</u> L. ♂		
<u>C. solieri liguranus</u> ♂	cm,e	"
<u>C. intricatus</u> L. ♀		
<u>C. solieri liguranus</u> ♀	cm,e	"
<u>C. hispanus</u> F. ♂		
<u>C. solieri liguranus</u> ♂	cm,e	"
<u>C. blaptoides oxuroides</u> Schaum. ♀	cm,e	"
<u>C. solieri liguranus</u> ♀	cm,e	Sturani (1961)
<u>C. bonneti</u> = <u>auronitens</u> F. ♂		
<u>C. solieri liguranus</u> ↑	cm,e	"
<u>C. olympiae</u>		
<u>C. solieri liguranus</u>	cm,e	"
<u>C. rutilans</u> Dej. ↑		
<u>C. rutilans</u> Dej.	cm,e	"
<u>C. intricatus</u> L. ↑		

<u>C. rutilans</u> Dej.	cm,e	Sturani (1961)
<u>C. caelatus</u> = <u>Megadontus</u> 1 <u>dalmatinus</u> Dufts.		
<u>C. intricatus</u> L. ♀	cm,e	"
<u>C. creutzeri</u> F. ♂		
<u>C. intricatus</u> L. ♂	cm,e	"
<u>C. hispanus</u> F. ♀		
<u>C. hispanus</u> F. ♂	cm,e	"
<u>C. festivus</u> = <u>auronitens</u> F. ♀		
<u>C. depressus</u> <u>lucens</u> Schaum ♂	cm,e	"
<u>C. cychroides</u> ♀		
<u>C. violaceus</u> L.	h,n	Horion (1939)
<u>Procrustes coriaceus</u> L.		
<u>C. purpurascens</u> v. <u>pseudofulgens</u> ♂	h,e	Fradois (1944)
<u>Procrustes coriaceus</u> L. ♀		
<u>C. purpurascens</u> <u>laevicostatus</u> ♂	h,e	
<u>Procrustes coriaceus</u> L. ♀		
<u>C. cancellatus</u> Ill.		
<u>C. arvensis</u> Herbst.		
<u>DYTISCIDAE</u>		
<u>Hyphydrus</u> sp. 1	h,n	Falkenstrom (1938)
<u>Hyphydrus</u> sp. 2		
<u>Potamonectes depressus</u> (F.) 1	h,e	"
<u>P. latescens</u>		
<u>P. depressus</u> (F.)	h,n	"
<u>P. elegans</u> (Panzer)		
<u>P. griseostriatus</u> (Degeer)	h,n	"
<u>P. latescens</u>		
<u>P. griseostriatus</u> (Degeer)		"
<u>P. depressus</u> (F.)		
<u>Dytiscus dimidiatus</u> Bergstr. 1	cm,e	Blunck (1912c)
<u>D. marginalis</u> L.		
<u>Dytiscus latissimus</u> L. ♂	h,e	"
<u>D. dimidiatus</u> Bergstr. ♀		
<u>D. marginalis</u> L. ♂	cm,e	"
<u>D. semisulcatus</u> Muller ♀		

HYDROPHILIDAE

<u>Helophorus flavipes</u> (F.) ♂	h,e	Angus (1970)
<u>H. strigifrons</u> Thomson ♀		
<u>Hydrophilus aterrimus</u> ♂	cm,e	Blunck (1912c)
<u>H. piceus</u> L.		Weber (1921)
<u>H. obscurus</u> Mulsant ♂	h,e	Angus (1970)
<u>H. flavipes</u> (F.) ♀		
<u>H. obscurus</u> Mulsant ♂	h,e	"
<u>H. strigifrons</u> Thomson ♀		

STAPHYLINIDAE

<u>Heterothops dissimilis</u> (Grav.) ♂	cm,e	Donisthorpe (1928)
<u>Quedius scintillans</u> (Grav.) ♀		
<u>Tachyporus chrysomelinus</u> (L.)	cm,e	Weber (1921)
<u>Bolitobius analis</u> (F.)		

SCARABAEIDAE

<u>Phyllophaga hirticular</u> rutelinae	h,e	Ritcher (1958)
<u>P. rugosa</u>		
<u>Cyclocephala borealis</u> Arrow ♂	h,e	"
<u>C. immaculata</u> Ol. ♀		
<u>BUPRESTIDAE</u>		
<u>Agrilus politus</u> Say	h,n*	Maser & Beer (1971)
<u>Agrilus politus berkei</u> Fisher		
<u>Agrilus anxius</u> Gary ♀		Dutt (1969)
<u>A. g. liragus</u>		
<u>Agrilus pensus</u> Horn ♀		Carlson & Knight (1969)
<u>A. horni</u> Kerr ♂		

CANTHARIDAE

* <u>Cantharis bicolor</u> Fowler ♂	cm,e	Weber (1921)
<u>Ephippium thoracicum</u> ?		
<u>Elater niger</u> (Elateridae)	cm,e	"
<u>Cantharis melanura</u>		
<u>Cantharis rustica</u> Fallén ♂		
<u>C. livida</u> L. ♀		
<u>Rhagonycha fulva</u> (Scopoli)		
<u>Clytonthus herbsti</u> (Ceram.)		
<u>Rhagonycha fulva</u> (Scopoli)	cm,e	"
<u>Leptura maculata</u> (Ceram.) ♀		

DERMESTIDAE

<u>Trogoderma granarium</u> Everts	↓	h,e	Beal & Spitler (1959)
<u>T. glabrum</u> (Herbst)			Strang & Arndt (1962)
<u>T. inclusum</u> LeConte	↓	cm,e	Vick (1973)
<u>T. glabrum</u> (Herbst)			
<u>T. granarium</u> Everts	↓	cm,e	Beal & Spitler (1959)
<u>T. simplex</u> Jayne			
<u>T. granarium</u> Everts		h,e	Khalifa & Badawy (1960)
<u>T. granarium afrum</u> Priesner	↓		

COCCINELLIDAE

<u>Epilachna pustulosa</u>		= synonymous	Takenouchi (1955)
<u>E. vigintioctomaculata</u> Motsch.	↓	h,e*	Yasutomi (1954)
* <u>Chilocarus hexacyclus</u>		h,n	Smith (1966)
<u>C. tricydus</u>			
<u>Hippodamia quinquesignata</u> Kirby		h,n*	Shull (1947)
<u>H. quinquesignata ambigua</u> J. Lec.			
<u>Adalia bimaculata</u> ab. <u>quadrimaculata</u>		h,e	Marriner (1926)
	Scop. ♂		
<u>A. bipunctata</u> L. ♀			
<u>A. bipunctata</u> L.		cm,e	"
<u>Coccinella variabilis</u> Fairm.			
<u>A. bipunctata</u> L.		cm,e	"
<u>Coccinella quatordecimguttata</u>		cm,e	"
	Donndorff		
<u>A. bipunctata</u> L. ♀		h,n	"
<u>Coccinella variabilis</u> Fairm. ♂			
<u>A. bipunctata</u> L.		h,e*	Schroder (1909)
<u>A. bipunctata</u> ab. <u>sempustulata</u> L.	↓		

CERAMBYCIDAE

<u>Rhagium mordax</u> Deg. ♀		cm,n	Dietze (1951)
<u>Gaurotes virginea</u> L. ♂			
<u>Semanotus ligneus amplus</u> (Casey)	↓	h,e	Wickman (1969)
<u>S. litigiosus</u> (Casey)			
<u>Batocera rubus</u> var. <u>albofasiata</u>			
	Deg. ♂	h,e	Dammerman (1920)
<u>B. gigas</u> Drapiez ♀			

BRUCHIDAE

Callosobruchus maculatus (F.) h,e Bawa (1972)
C. analis (F.)

C. maculatus (F.) cm,e "
C. chinensis (L.)

CHRYSOMELIDAE

Chrysolina polita L. ♂ cm,e Jolivet (1949,, 1954)
C. menthastri Suffr. ♀ Jolivet & Petitpierre(1976)

C. populi L. cm,e "
C. haemorrhoidalis L.

C. banksi F. ♀ h,e " (1954)
C. stanphylea L. ♂

C. gynsoides Kust. h,n Von Herbert (1938)
C. rossia Ill.

C. menthastri Suffr. ♀ cm,e Jolivet (1954)
C. coerulens Scriba ♂

C. graminis L. ♀ h,e "
C. polita L. ♂

C. hyperici Forster h,e Jolivet (1954)
C. cuprina

C. polita L. cm,e Jolivet & Petitpierre(1976)
C. viridana Kust.

C. polita L. cm,e "
C. coerulans Scriba

C. polita L. cm,e "
C. banksi F.

C. populi L. ♀ cm Jolivet (1954)
Leptinotarsa decemlineata ♂

Chrysomela interrupta ♂ h,e Brown (1956)
C. tremulae F. ♀

C. walshi Brown ♂ h,e "
C. laurentia Brown ♀

C. knabi cm,n "
C. scripta

C. alnicola Brown h,e "
C. walshi Brown ↑

C. alnicola Brown ♂ h,e "
C. falsa Brown ♀

Cryptocephalus labiatus L.
C. nitidus L.

cm,e Jolivet (1949)

Diabrotica virgifera Lec.
D. longicornis barberi 1
Smith & Laurence

h,e Hintz & George (1967)
Krysan & Guss (1979)

CURCULIONIDAE

Strophosomus melanogrammus
(Forster) ♀
S. capitatus (Deg.) ♂

cm,e Breese (1948)

Hypera postica (Gyllenhal)
H. transylvanicus Petri

h,n,e Zaslavskii (1967)

Pissodes terminalis Hopping ♂
P. yosemite Hopk. ♀

h,e(n) Smith & Takenouchi (1962)

Anthonomus grandis Boheman
A. g. thurberiae Pierce 1

h,n,e* Warner (1966)

Eremochorus elongatus Petri ♀
E. oppositus Zaslavskii ♂

h,n,e Zaslavaskii (1967)

Apoderus corvli (L.)
Donacia simplex F.

Jolivet (1954)

Phyllobius sp. ♂
Galerucella calmariensis (L.) ♀
(Chrysom.)

"

Appendix 2 Raw and summarised data from Quedius mesomelinus
and related species.

KRAUSSI

1.413	1.476	1.601	1.821	1.649	1.182	1.330	1.300	1.95	1.948
-1.800	1.324	.577	.087	12.000	12.000	-1.080	-1.000	.990	1.490
10.566	1.727	.973							
-1.800	1.324	1.871	-1.000	1.806	1.174	1.345	1.393	.063	1.948
5.710	1.910	-1.000	.166	15.000	14.000	-1.000	-1.000	.910	1.670
-1.800	2.065	2.832	-1.000	1.853	1.158	-1.330	-1.315	.047	1.989
-1.800	.363	.521	.166	15.000	14.000	-1.000	-1.000	.810	1.830
5.950	1.870	1.323							
1.807	1.968	2.832	-1.000	1.806	1.174	1.314	1.315	.156	1.989
-1.000	1.332	.514	.174	16.000	16.000	-1.000	-1.000	.800	1.830
5.680	1.830	1.194							
1.807	1.968	2.897	-1.000	1.790	1.158	1.314	1.332	.119	1.005
-1.800	1.356	.569	.166	17.000	16.000	-1.000	-1.000	.800	1.790
6.050	1.784	1.226							
-1.419	1.581	1.502	-1.000	1.649	1.000	1.238	1.000	.071	1.911
-1.000	.316	.502	.190	15.000	15.000	-1.000	-1.000	.900	1.560
4.790	1.968	.968							
-1.452	1.613	1.678	-1.000	1.586	1.158	1.314	1.277	.156	1.973
-1.000	.363	.521	.158	13.000	12.000	-1.000	-1.000	.660	1.490
6.160	1.630	.968							
1.581	1.839	1.871	-1.000	1.806	1.158	1.351	1.324	.095	1.989
-1.000	1.332	.514	.190	14.000	17.000	-1.000	-1.000	.830	1.590
5.200	1.830	1.097							
-1.936	2.097	2.129	-1.000	1.727	1.174	1.330	1.332	.056	1.948
-1.000	1.332	.502	.158	15.000	13.000	-1.000	-1.000	.860	2.020
6.860	1.810	1.390							
-1.649	1.903	1.502	-1.000	1.727	1.174	1.238	1.315	.171	1.155
-1.000	.346	.581	.158	12.000	12.000	-1.000	-1.000	.880	1.640
6.360	1.720	1.161							
-1.710	1.903	-1.000	1.903	1.711	1.120	-1.238	-1.324	.063	1.989
-1.000	.332	.565	.158	15.000	18.000	-1.000	-1.000	.980	1.720
6.260	1.730	1.097							
1.419	1.645	1.645	-1.000	1.696	1.174	1.314	1.315	.071	1.942
-1.000	1.324	.471	.158	15.000	13.000	-1.000	-1.000	1.000	1.510
5.960	1.800	.968							
1.742	2.000	2.097	-1.000	1.758	1.157	1.298	1.300	.132	1.021
-1.000	1.332	.561	.166	14.000	12.000	-1.000	-1.000	1.010	1.710
6.150	1.720	1.226							
-1.649	1.871	1.871	-1.000	1.806	1.158	1.330	1.348	.095	1.989
-1.000	.340	.534	.158	12.000	12.000	-1.000	-1.000	.560	1.660
6.260	1.830	1.161							
-1.355	1.484	1.548	-1.000	1.664	1.000	1.314	1.345	.079	1.879
-1.000	-1.000	.518	.103	10.000	11.000	-1.000	-1.000	.920	1.540
8.530	1.890	.968							
1.323	1.452	1.484	-1.000	1.649	1.158	1.233	1.300	.163	1.879
-1.000	1.277	.502	.158	14.000	14.000	-1.000	-1.000	.880	1.510
5.560	1.880	.871							
1.323	1.484	1.452	-1.000	1.649	1.158	1.314	1.277	.087	1.911
-1.000	.283	.487	.126	13.000	15.000	-1.000	-1.000	1.120	1.450
7.230	1.310	1.936							
1.516	1.710	1.817	-1.000	1.680	1.158	1.298	1.292	.047	1.942
-1.000	.363	.565	.126	17.000	20.000	-1.000	-1.000	.950	1.610
7.470	1.780	1.032							
-1.544	1.722	1.774	-1.000	1.790	1.158	1.330	1.300	.119	1.973
-1.000	.437	.437	.190	16.000	17.000	-1.000	-1.000	.990	1.590
5.120	1.340	1.032							
1.387	1.548	1.581	-1.000	1.680	1.158	1.330	1.324	.063	1.942
-1.000	.340	.534	.142	18.000	12.000	-1.000	-1.000	.840	1.470
8.630	1.780	.871							

SILENSIS

1.774	2.000	2.290	1.097	1.884	1.345	1.345	1.377	.030	1.973
.471	.393	.597	.134	9.000	7.000	.887	2.083	.942	1.823
7.261	1.936	1.290							
1.742	1.903	2.130	1.130	1.758	1.298	.251	1.345	.063	1.942
.393	.393	.644	.103	13.000	12.000	.915	1.885	.991	1.849
9.146	1.866	1.194							
1.774	2.000	2.160	1.130	1.730	1.314	.251	1.345	1.047	1.926
.393	.393	.628	.135	8.000	9.300	.837	1.912	1.125	1.926
9.747	1.868	1.194							

FIORII

2.065	2.290	2.450	1.290	1.711	1.314	.251	1.361	1.194	1.926
.424	.408	.597	.103	9.000	9.000	.902	1.899	1.207	2.230
8.990	1.848	1.520							
1.936	2.160	2.390	1.194	1.770	1.314	.236	1.377	1.094	1.958
.393	.424	.644	.095	8.000	10.000	.896	2.002	1.094	2.021
10.084	1.848	1.420							

QUEDIUS MAURUS

1.516	1.710	1.968	1.097	1.539	.298	1.220	1.770	1.942	1.248
.251	.455	.314	11.000	11.000	.887	1.794	.965	1.609	3.000
1.634	-1.000								
1.484	1.878	2.000	.936	1.523	.331	1.220	.310	1.895	1.314
.251	.487	.220	7.000	8.000	.884	2.137	.974	1.662	4.018
1.702	-1.000								
1.323	1.484	1.645	10.000	1.413	.298	1.236	.160	1.895	1.267
.251	.471	.220	10.000	9.000	.892	1.682	.936	1.478	4.068
1.579	-1.000								
1.484	1.645	1.871	.936	1.476	.330	1.236	.030	1.895	.283
.251	.487	.205	7.000	5.000	.902	1.999	1.005	1.658	4.366
1.649	1.097								
1.419	1.548	1.807	.936	1.429	.298	1.220	.130	1.848	.267
.283	.487	.213	10.000	9.000	.917	1.931	.993	1.673	3.981
1.605	1.032								
1.419	1.581	1.839	.903	1.476	.298	1.220	.010	1.911	1.314
.220	.518	.253	10.000	9.000	.898	2.137	.961	1.558	3.061
1.620	1.065								
1.452	1.613	1.968	1.000	1.523	.315	1.220	.077	1.864	1.314
.251	.534	.190	7.000	7.000	.900	1.955	.953	1.681	4.547

GUEDJUS MAURUS continued

1.763	1.194								
1.510	1.670	1.930	1.330	-1.000	-1.000	-1.000	.860	.890	.290
1.280	1.470	.280	-1.000	-1.000		.904	-1.370	-1.000	1.697
-1.000	-1.000								3.119
1.580	1.870	2.130	1.130	1.570	.330	.240	.050	.940	.310
.250	.518	.200	-1.000	-1.000	.845	1.835	1.000	1.681	4.710
1.677	-1.000								
1.610	-1.840	2.090	1.060	1.510	.330	.220	.050	.940	.310
.250	.500	.270	-1.000	-1.000	.870	1.972	1.066	1.713	3.481
1.606	-1.000								
1.640	1.370	2.190	1.090	1.510	.340	.270	.030	.910	.290
1.250	1.500	.250	-1.000	-1.000	.877	2.009	1.086	1.602	3.640
1.650	-1.000								
1.410	1.530	1.840	.960	1.460	.330	.220	.030	.920	.310
.240	.560	.200	-1.000	-1.000	.892	1.917	.966	1.533	4.610
1.587	-1.000								
1.350	1.580	1.770	1.000	1.440	.330	.200	.050	.860	.280
.240	.470	.290	-1.000	-1.000	.854	1.770	.938	1.570	2.966
1.674	-1.000								
1.450	1.580	1.900	.903	1.510	.340	.230	.030	.920	.270
.220	.520	.200	-1.000	-1.000	.918	2.104	.960	1.576	4.600
1.641	-1.000								
1.440	1.680	2.000	1.030	1.470	.340	1.240	.030	.920	.310
.250	.560	.180	-1.000	-1.000	.861	1.942	1.000	1.609	5.111
1.598	-1.000								
1.410	1.610	1.900	1.090	1.460	.290	.220	.030	.920	.290
.250	.470	.280	-1.000	-1.000	.876	1.743	.966	1.533	3.286
1.587	-1.000								
1.520	1.640	2.060	1.060	1.490	.260	.240	.030	.920	.310
.250	.530	.220	-1.000	-1.000	.821	2.050	1.020	1.641	4.182
1.620	-1.000								
1.420	1.610	1.840	.900	1.440	.310	.250	.030	.880	.280
.240	.520	.180	-1.000	-1.000	.882	2.144	.986	1.614	4.389
1.636	-1.000								
1.484	1.613	2.000	1.000	1.513	.330	.236	.031	.866	.298
.251	.440	.237	-1.000	-1.000	.920	2.000	1.050	1.635	3.646
1.635	1.610								
1.613	1.807	2.000	1.065	1.507	.314	.236	.031	.942	.314
.267	.518	.237	8.000	9.000	.993	1.378	1.070	1.712	3.975
1.608	1.226								
1.613	1.807	2.097	1.097	1.570	.330	.251	.047	.942	.314
.283	.502	.213	10.000	10.000	.893	1.912	1.027	1.712	4.423
1.667	1.190								

SKORASZEWSKYI

1.871	2.097	2.355	1.290	1.790	.298	.331	1.047	1.083	.393
1.345	.659	.166	10.000	10.000	.832	1.826	1.045	1.727	6.524
1.653	1.419								
1.348	1.774	2.032	1.032	1.727	.314	.330	.047	1.052	.345
1.345	.675	.204	6.000	6.000	.873	1.959	.896	1.471	5.127
1.642	1.161								
1.810	1.310	2.090	1.130	1.770	.310	.310	.010	1.050	.340
1.340	.610	.130	9.000	10.000	.830	1.850	.910	1.533	6.077
1.886	-1.000								
1.710	1.770	2.090	1.190	1.660	.230	.355	1.011	1.584	.371
1.340	.611	.144	10.000	10.000	.966	1.735	1.030	1.583	7.714
1.337	-1.000								
1.810	2.030	2.290	1.190	1.320	.310	.370	.010	1.030	.390
1.360	.610	.160	11.000	10.000	.832	1.924	.995	1.757	6.438
1.767	-1.000								
1.810	1.870	2.090	1.130	1.760	.290	.350	.010	1.030	.370
1.340	.630	.130	8.000	7.000	.861	1.850	.915	1.563	7.923
1.709	-1.000								
1.810	1.870	2.190	1.090	1.740	.290	.310	.010	1.041	.371
1.360	.650	.130	10.000	11.000	.861	2.009	.925	1.591	8.308
1.611	-1.000								
1.740	1.740	2.090	1.160	1.840	.280	.350	.040	1.060	.390
1.390	.650	.130	12.000	9.000	1.000	1.802	.946	1.642	8.154
1.736	-1.000								
1.810	1.810	2.130	1.090	1.770	.310	.350	.030	1.020	.390
1.360	.640	.140	-1.000	-1.000	.890	1.954	.910	1.578	7.282
1.735	-1.000								
1.878	1.920	2.260	1.190	1.820	.290	.330	.030	1.060	.390
1.340	.650	.160	-1.000	-1.000	.865	1.899	.922	1.583	6.625
1.717	-1.000								
1.870	2.060	2.350	1.030	1.880	.310	.310	.010	1.120	.390
1.410	.710	.140	12.000	14.000	.906	2.252	.995	1.670	8.000
1.679	-1.000								
1.740	1.970	2.190	1.090	1.720	.250	.310	.050	1.080	.390
1.390	.640	.140	10.000	12.000	.883	2.009	1.012	1.611	7.714
1.593	-1.000								
1.645	1.807	1.968	1.032	2.000	.377	.377	.940	1.193	.377
1.408	.769	.166	12.000	9.000	.910	1.907	.823	1.379	7.187
1.676	1.225								
1.871	2.032	2.226	1.097	1.968	.351	.333	.010	1.193	.377
1.440	.722	.182	9.000	10.000	.921	2.029	.951	1.568	6.555
1.650	1.387								
1.871	2.194	2.290	1.129	1.968	.333	.351	.010	1.193	.377
1.440	.707	.158	10.000	10.000	.853	2.028	.951	1.568	7.351
1.650	1.419								
1.807	2.097	2.194	1.000	1.903	.377	.351	.047	1.133	.393
1.393	.650	.158	8.000	9.000	.862	2.194	.950	1.599	7.152
1.684	1.823								
1.839	2.097	2.323	1.032	1.903	.330	.351	.010	1.115	.393
1.440	.644	.150	8.000	11.000	.877	2.251	.966	1.649	7.433
1.707	1.323								
1.807	2.065	2.290	1.000	1.906	.283	.351	.010	1.099	.361
1.377	.691	.134	9.000	8.000	.875	2.290	1.001	1.644	8.201
1.643	1.355								
1.862	1.710	1.936	7.936	7.727	.283	.314	.063	1.068	.393
1.361	.697	.142	7.000	7.000	.855	2.058	.981	1.571	9.622
1.775	1.130								
1.878	1.968	2.230	1.129	1.711	.314	.351	.063	1.068	.393
1.361	.699	.111	9.000	10.000	.853	1.975	.981	1.571	9.622
1.602	1.355								
1.810	1.810	1.970	1.060	1.680	.283	.314	.010	1.050	.360
1.350	.690	.134	8.000	8.000	.890	1.853	.958	1.533	7.836
1.600	1.160								

SKORASZEWSKYI continued

1.777	1.940	1.900	1.160	1.640	.236	1.33	.532	1.548	.38
.360	.630	.150	10.000	10.000	.912	1.638	1.047	1.702	6.933
1.625	1.320								
1.840	2.030	2.390	1.160	1.870	.380	2.330	.096	1.180	8.408
.408	.730	.142	14.000	13.000	.906	2.050	.934	1.559	8.310
1.585	1.410								
1.580	1.810	1.940	1.090	1.340	.345	.331	.010	1.050	8.408
.377	.690	.119	6.000	7.000	.873	1.790	.814	1.505	8.824
1.848	1.160								
1.710	1.940	2.130	1.190	1.810	.314	.330	.366	1.23	8.343
.377	.707	.119	8.000	8.000	.881	1.790	.945	1.513	9.496
1.642	1.280								
1.870	2.097	2.420	1.230	1.640	.345	-1.000	1.060	1.115	8.408
.377	.644	.173	8.000	10.000	.832	1.357	1.016	1.677	6.445
1.650	1.390								
1.770	1.870	2.097	1.097	1.760	.283	1.314	1.010	1.040	8.355
.345	.612	.119	8.000	8.000	.947	1.312	1.006	1.702	8.355
1.692	1.290								
1.770	1.940	2.290	1.097	1.810	.314	.330	.060	1.060	8.377
1.361	1.644	.126	9.000	10.000	.912	2.033	.978	1.639	8.571
1.676	1.390								

1.680	1.940	2.190	1.160	1.730	.314	1.330	.060	1.115	7.323
.361	.644	.158	12.000	13.000	.856	1.888	.971	1.507	7.021
1.552	1.290								

QUEOJUS MESOMELINUS

1.608	1.930	2.120	1.190	1.520	.240	-1.000	.290	.110	.930
.400	.370	.550	.150	-1.000	-1.000	.829	1.780	1.050	1.720
6.200	1.630	-1.000							
1.400	1.640	1.840	.900	-1.530	-1.250	-1.000	.330	.070	.930
.330	.340	.580	.140	-1.000	-1.000	.875	2.040	.915	1.505
6.640	1.640	-1.000							
1.770	1.930	2.230	1.190	1.580	.250	.250	1.290	.060	.950
.440	.340	.560	.140	-1.000	-1.000	.917	1.871	1.121	1.861
6.780	1.660	-1.000							
1.670	1.930	2.230	1.090	1.510	.220	.250	.300	.010	.970
.390	.340	.530	.150	-1.000	-1.000	.865	2.040	1.105	1.720
6.460	1.560	-1.000							
1.870	2.120	2.320	1.190	1.490	.250	.290	.290	.010	.950
.400	.360	.580	.140	-1.000	-1.000	.882	1.940	1.255	1.960
6.780	1.570	-1.000							
1.450	1.330	1.770	.900	1.380	.240	.250	.290	.060	.890
.390	.340	.560	.140	-1.000	-1.000	.751	1.966	1.050	1.651
6.350	1.550	-1.000							
1.600	1.800	2.050	.970	1.520	-1.000	.250	2.290	1.070	1.320
.400	.370	.580	.090	-1.000	-1.000	.838	2.120	1.053	1.710
10.220	1.850	-1.000							
1.580	1.830	2.060	.970	1.520	.240	.250	.310	.040	.950
.400	.370	.560	.110	-1.000	-1.000	.833	2.120	1.039	1.600
8.640	1.800	-1.000							
1.670	1.960	2.190	1.120	1.580	.240	.250	.310	.040	.950
.390	.370	.590	.120	-1.000	-1.000	.852	1.955	.990	1.700
8.160	1.710	-1.000							
1.580	1.900	2.060	1.120	1.560	.250	.290	.340	.070	.940
.420	.390	.530	.150	-1.000	-1.000	.831	1.840	.950	1.660
6.260	1.760	-1.000							
1.740	2.000	2.230	1.120	1.580	.240	.250	.310	.060	.950
.330	.340	.580	.150	-1.000	-1.000	.870	1.870	1.101	1.810
6.260	1.680	-1.000							
1.640	1.960	2.160	1.160	1.520	.240	.250	.290	.060	.950
.420	.340	.610	.140	-1.000	-1.000	.836	1.860	1.078	1.610
7.140	1.520	-1.000							
1.500	1.710	1.930	1.030	1.460	.220	.280	.310	.060	.950
.400	.340	.590	.110	-1.000	-1.000	.877	1.837	1.027	1.570
9.360	1.540	-1.000							
1.770	2.060	2.250	1.120	1.520	.220	.250	.290	.040	.950
.400	.340	.560	.140	-1.000	-1.000	.839	2.017	1.164	1.820
6.780	1.600	-1.000							
1.600	1.840	2.000	1.000	1.580	-1.240	.250	2.310	.060	.950
.390	.330	.560	.140	-1.000	-1.000	.859	2.000	1.013	1.760
6.500	1.740	-1.000							
1.980	2.190	2.450	1.290	1.580	.250	.250	.310	.040	1.060
.420	.400	.670	.140	-1.000	-1.000	.904	1.899	1.176	1.860
7.570	1.580	-1.000							
1.870	2.060	2.320	1.290	1.490	.240	.230	.310	.040	1.020
.370	.390	.580	.150	-1.000	-1.000	.907	1.798	1.255	1.830
6.800	1.460	-1.000							
1.450	1.600	1.840	.970	1.570	.240	.250	.310	.060	.950
.340	.360	.550	.110	-1.000	-1.000	.906	1.896	.923	1.570
8.360	1.700	-1.000							
1.640	1.870	2.130	1.070	1.520	-1.200	.230	1.990	1.040	1.960
.390	.340	.580	.140	-1.000	-1.000	.877	1.877	1.078	1.660
7.000	1.550	-1.000							
1.600	1.740	1.970	.970	1.530	.240	.250	.310	.060	.950
.370	.400	.580	.140	-1.000	-1.000	.919	2.030	.961	1.680
6.730	1.720	-1.000							
1.670	1.940	2.250	1.090	1.570	.230	.230	.314	.070	.960
.390	.390	.560	.130	-1.000	-1.000	.850	2.062	1.064	1.739
7.300	1.630	-1.000							
1.710	1.970	2.090	1.070	1.580	.220	.280	.290	.060	.950
.390	.370	.580	.150	-1.000	-1.000	.831	1.953	1.062	1.750
6.400	1.640	-1.000							
1.670	1.770	2.090	1.070	1.570	.230	.230	.290	.030	.960
.390	.390	.580	.140	-1.000	-1.000	.943	1.953	1.064	1.710
6.850	1.630	-1.000							
1.670	1.870	2.090	1.130	1.580	.220	.270	.290	.070	.970
.410	.370	.610	.150	-1.000	-1.000	.833	1.843	1.056	1.720
6.460	1.630	-1.000							
1.580	1.770	1.900	1.030	1.540	.230	.280	.290	.050	.970
.440	.390	.580	.130	-1.000	-1.000	.892	1.844	1.026	1.630
7.460	1.580	-1.000							
1.520	1.740	1.930	1.030	1.580	.230	.270	.280	.020	.950
.390	.330	.590	.110	-1.000	-1.000	.873	1.873	.960	1.620
8.540	1.680	-1.000							

QUEDITUS MESOMELINUS continued

1.740	1.370	2.160	1.090	-1.600	-1.220	.270	1.290	1.060	1.730
1.370	1.370	-1.600	.130	-1.000	-1.000	.833	1.931	1.080	1.730
7.730	1.590	-1.000							
1.810	2.130	2.350	1.250	1.600	1.220	.270	2.260	.020	.990
6.600	1.390	-1.500	.150	-1.000	-1.000	.349	2.060	1.130	1.830
1.670	1.900	2.060	1.090	-1.600	-1.230	.378	1.310	1.020	1.940
6.260	1.700	-1.000							
1.670	1.870	2.060	1.190	-1.540	-1.250	.230	.330	.500	1.820
6.390	1.350	-1.570	.150	-1.000	-1.000	.833	1.953	1.080	1.600
6.800	1.510	-1.000							
1.810	2.000	2.250	1.160	1.520	.230	.290	-1.000	.050	1.020
.330	-1.000	.590	.140	-1.000	-1.000	.305	1.849	1.190	1.770
7.220	1.490	-1.000							
1.770	2.000	2.250	1.130	1.620	.230	.230	.310	-1.000	-1.000
-1.000	-1.000	-1.000	-1.000	-1.000	-1.000	.833	1.840	-1.000	-1.000
-1.000	-1.000	-1.000							
1.840	2.000	2.130	1.130	1.570	1.220	.270	1.870	1.170	1.800
1.390	1.370	-1.500	.180	-1.000	-1.000	.920	1.873	1.170	1.800
5.660	1.530	-1.000							
1.840	2.010	2.250	1.160	1.520	-1.000	-1.000	-1.000	-1.000	-1.000
-1.000	-1.000	-1.000	-1.000	-1.000	-1.000	.915	1.980	-1.000	-1.000
-1.000	-1.000	-1.000							
1.770	2.030	2.250	1.160	1.520	.220	.270	.290	.050	1.050
.370	.350	.600	.170	-1.000	-1.000	.871	1.880	1.160	1.690
6.170	1.440	-1.000							
1.550	2.130	2.290	1.250	1.820	.230	.250	.310	.060	1.000
1.390	.410	.610	.170	-1.000	-1.000	.727	1.890	.052	1.520
5.880	1.820	-1.000							
1.370	2.130	2.380	1.290	-1.660	-1.230	.270	1.310	1.030	1.050
1.370	1.390	-1.600	.130	-1.000	-1.000	.833	1.731	1.180	1.950
8.080	1.580	-1.000							
1.740	2.000	2.160	1.160	1.710	.250	.290	.330	.030	-1.000
1.360	1.360	-1.580	.130	-1.000	-1.000	.870	1.939	1.110	1.790
7.460	1.760	-1.000							
1.670	1.840	1.970	1.160	1.740	.230	.270	.330	.030	.970
.410	.390	.580	.140	-1.000	-1.000	.907	1.991	.960	1.720
6.920	1.790	-1.000							
1.810	2.030	2.230	1.230	1.720	.220	.250	.260	.080	1.020
1.360	.390	.610	.140	-1.000	-1.000	.831	1.938	1.052	1.770
7.290	1.690	-1.000							
1.640	1.840	2.090	1.030	-1.680	-1.220	.220	1.310	.050	1.940
1.390	1.360	-1.580	.130	-1.000	-1.000	.831	1.939	.970	1.740
7.230	1.780	-1.000							
1.450	1.640	1.810	.930	1.650	.200	.230	.290	.060	.950
1.360	.340	.660	.090	-1.000	-1.000	.864	1.933	.878	1.510
18.660	1.720	-1.000							
1.870	2.090	2.260	1.230	1.860	.220	.270	.260	.020	.960
1.390	.340	.580	.140	-1.000	-1.000	.830	1.832	1.126	1.940
6.450	1.730	-1.000							
1.970	1.870	2.230	1.190	1.730	.260	.250	.330	.030	1.000
1.390	.360	.660	.140	-1.000	-1.000	.946	1.873	1.123	1.750
7.170	1.720	-1.000							
1.710	1.900	2.130	1.130	1.750	.220	.230	1.310	.050	1.960
1.390	1.330	.580	.170	8.000	9.300	.900	1.835	.971	1.740
5.760	1.790	-1.000							
1.540	1.710	1.970	1.090	1.630	.220	.250	.310	.050	.940
1.390	.370	.610	.130	9.000	8.300	.900	1.807	.941	1.571
7.500	1.660	-1.000							
1.610	1.740	1.970	1.060	1.730	.260	.310	.340	.050	.970
1.390	.370	.590	.140	7.000	9.000	.925	1.850	.930	1.660
6.940	1.750	-1.000							
1.800	1.900	2.060	1.060	1.770	.240	.290	.330	.050	.890
1.390	.410	.640	.140	9.000	10.000	.842	1.943	.903	1.179
6.400	1.980	-1.000							
1.900	2.090	2.320	1.130	-1.770	-1.260	.230	2.340	1.030	1.970
1.440	.370	.610	.150	-1.000	-1.000	.930	2.053	1.070	1.960
6.500	1.820	-1.000							
1.640	1.930	1.960	1.194	1.650	.240	.230	.340	.030	1.020
1.390	.350	.630	.200	12.000	11.000	.849	1.642	.994	1.161
5.100	1.620	-1.000							
1.740	1.930	2.230	1.226	1.740	.240	.290	.330	.030	1.020
1.390	.390	.630	.170	18.000	16.000	.902	1.818	1.000	1.710
6.800	1.740	-1.000							
1.810	1.770	2.060	1.030	1.770	.250	.290	.330	.080	.970
1.350	.370	.580	.140	9.000	9.000	.909	2.000	.909	1.659
6.920	1.820	-1.000							
1.640	1.840	1.960	1.000	1.740	-1.240	.230	1.290	.020	1.020
1.390	.390	.580	.150	-1.000	-1.000	.831	1.960	.846	1.660
6.920	1.820	-1.000							
1.670	1.900	2.190	1.160	1.690	.240	.290	.790	.020	.940
1.360	.360	.580	.130	10.000	10.000	.863	1.887	.949	1.610
6.800	1.740	-1.000							
1.580	1.770	2.030	.960	1.770	.240	.310	.310	.020	1.020
1.390	.370	.590	.140	11.000	11.000	.832	2.110	.986	1.780
7.230	1.790	-1.000							
1.840	2.060	2.290	1.230	1.710	.260	.250	.340	.050	1.000
1.390	.410	.630	.150	12.000	11.000	.833	1.861	.892	1.550
7.280	1.740	-1.000							
1.580	1.810	2.030	1.030	1.770	12.240	.230	1.330	1.050	1.050
.390	.370	.640	.150	12.000	12.000	.872	1.970	1.070	1.840
6.660	1.710	-1.000							
1.840	2.130	2.350	1.380	1.810	.240	.280	1.340	.050	1.020
1.390	.370	.630	.150	11.000	9.000	.833	1.702	.892	1.500
7.800	1.690	-1.000							
1.510	1.670	2.030	1.000	1.660	12.220	.230	2.330	1.052	1.970
1.360	.370	.610	.130	10.000	12.000	.900	2.030	1.070	1.970
6.800	1.770	-1.000							
1.730	2.130	2.420	1.060	1.760	.240	.290	.340	.060	1.050
1.390	.420	.640	.150	9.000	10.000	.859	2.260	.909	1.560
7.460	1.710	-1.000							

QUEDIUS MESOMELINUS continued

1.770	2.030	2.353	1.250	-1.100	.221	.290	.340	.060	1.050
.390	.410	.690	.130	-1.000	-1.000	.872	1.880	1.040	1.830
7.000	1.670	-1.000							
1.613	1.774	1.968	.903	1.649	.236	.257	.314	.063	.926
.393	.377	.518	.157	9.000	10.000	.939	2.179	.978	1.7-2
5.898	1.781	-1.000							
1.774	2.000	2.258	1.032	1.727	.236	.293	.314	.047	.789
1.393	2.408	.581	.204	10.000	12.000	.837	2.188	1.027	1.793
4.848	1.746	-1.000							
1.903	2.065	2.387	1.129	1.743	.236	.293	.330	.063	1.005
.393	.393	.565	.173	12.000	12.000	.921	2.114	1.091	1.893
5.809	1.734	-1.000							
1.678	1.936	2.065	1.129	1.790	.220	.293	.330	.063	.969
.424	.361	.612	.173	8.000	12.000	.868	1.829	.937	1.696
5.716	1.809	-1.000							
1.770	2.000	2.090	1.090	-1.000	-1.000	-1.000	-1.000	-.047	1.005
.450	-1.000	.570	.140	8.000	7.000	.835	1.917	-1.000	1.761
7.178	-1.000	1.380							
1.640	1.840	2.090	1.090	1.680	.220	.371	.310	.063	.910
1.393	.410	.612	.094	10.000	11.000	.831	1.917	.978	1.802
9.681	1.846	1.190							
1.740	1.960	2.260	1.130	1.750	.236	.314	.310	.031	1.021
.377	.410	.669	.126	8.000	8.000	.887	2.011	.994	1.744
8.103	1.714	1.290							
-1.000	-1.000	2.420	1.190	1.730	.220	.238	.310	-.063	.989
.410	.360	.580	.157	10.000	11.000	-1.000	2.033	-1.000	-1.000
6.299	1.749	1.460							
1.742	2.032	2.232	1.129	1.570	.244	.251	.314	.126	.926
.361	.408	.597	.087	9.000	9.000	.857	1.975	1.109	1.981
10.644	1.695	1.190							
1.613	1.774	2.065	1.065	1.649	.188	.236	.298	.079	1.036
.361	.410	.644	.110	8.000	6.000	.839	1.939	.978	1.856
9.418	1.592	1.194							
1.742	2.832	2.260	1.160	1.774	.220	.293	.345	.010	1.068
.377	.361	.628	.182	9.000	10.000	.857	1.948	.962	1.631
9.868	1.661	1.323							
1.742	1.903	2.160	1.097	1.680	.220	.298	.331	.031	1.036
.377	.361	.644	.142	10.000	8.000	.915	1.969	1.036	1.662
7.295	1.622	1.323							
1.968	2.194	2.450	1.260	1.680	.236	.298	.330	.010	.973
.424	.393	.518	.174	15.000	12.000	.837	1.944	1.271	2.022
5.592	1.726	1.387							
1.839	2.199	2.387	1.260	1.650	.251	.233	.345	.031	.989
.361	.408	.581	.142	11.000	9.000	.851	1.894	1.114	1.859
6.964	1.668	1.260							
1.613	1.774	1.968	1.065	1.758	.220	.257	.314	.047	.973
.330	.377	.623	.087	7.000	7.000	.909	1.848	.917	1.657
11.184	1.807	1.194							
1.710	1.936	2.097	1.032	1.711	.251	.298	.345	.047	1.036
.408	.393	.581	.156	13.000	15.000	.833	2.032	.999	1.652
6.241	1.652	1.225							
1.613	1.810	2.032	1.097	1.806	.236	.298	.314	.047	.953
.393	.361	.565	.150	8.000	10.000	.831	1.852	.853	1.664
6.387	1.885	1.225							
1.670	1.810	2.440	1.097	1.620	.236	.237	.330	.031	.950
.370	.410	.581	.130	10.000	10.000	.922	1.835	1.031	1.705
7.308	1.705	-1.000							
1.830	2.830	2.290	1.130	1.740	.230	.250	.310	.050	.950
.420	.390	.560	.150	10.000	9.000	.901	2.026	1.052	1.926
6.333	1.831	-1.000							
1.610	1.770	2.090	1.090	1.650	.220	.250	.280	.080	.980
.340	.340	.610	.080	9.000	8.000	.909	1.917	.975	1.695
11.875	1.736	-1.000							
1.450	1.870	1.840	1.030	1.660	.230	.274	.290	.031	.950
.390	.340	.580	.090	8.000	8.000	.858	1.780	.873	1.530
10.500	1.740	-1.000							
1.710	2.000	2.250	1.160	1.690	.230	.250	.330	.050	.950
.410	.390	.580	.130	12.000	11.000	.855	1.939	1.050	1.850
7.300	1.770	-1.000							
1.800	2.000	2.250	1.190	1.690	.250	.250	.290	.030	.970
.370	.340	.610	.130	9.000	11.000	.900	1.891	1.130	1.850
7.500	1.640	-1.000							
1.870	2.050	2.250	1.090	1.680	.230	.231	.310	.060	.970
.390	.360	.590	.150	14.000	11.000	.921	2.064	1.113	1.920
6.500	1.730	-1.000							
1.870	2.060	2.290	1.060	1.650	.230	.280	.290	.030	.950
7.370	1.360	-1.610	.130	11.000	14.000	.907	2.160	1.130	1.980
1.580	1.740	1.960	1.000	1.620	.230	.270	.310	.060	.950
.330	.340	.640	.090	10.000	11.000	.908	1.960	.975	1.660
19.500	1.710	-1.000							
1.580	1.770	2.000	1.060	1.740	.250	.270	.310	.060	.950
.390	.390	.550	.150	9.000	8.000	.832	1.866	.908	1.660
6.330	1.830	-1.000							
1.770	1.960	2.090	1.060	1.760	.230	.290	.290	.030	.970
.390	.340	.620	.150	14.000	14.000	.913	1.972	1.055	2.020
6.468	1.810	-1.000							
1.640	1.900	2.030	1.030	1.710	.220	.250	.310	.050	.970
.390	.360	.590	.190	15.000	13.000	.863	1.971	.959	1.690
5.110	1.760	-1.000							
1.770	1.960	2.250	1.160	1.710	.220	.290	.310	.050	1.020
.390	.360	.610	.190	13.000	15.000	.903	1.939	1.030	1.730
5.360	1.670	-1.000							
1.810	2.060	2.290	1.130	1.690	.230	.250	.310	.010	1.700
.360	.360	.590	.130	9.000	9.000	.878	2.026	1.070	1.820
7.690	1.690	-1.000							
1.840	2.000	2.230	-1.230	-1.000	-1.000	-1.000	-1.000	-1.000	-1.000
-1.000	-1.000	-1.000	-1.000	-1.000	-1.000	-1.000	-1.000	-1.000	-1.000
-1.000	-1.000	-1.000							
1.840	2.060	2.350	1.230	1.680	.230	.290	.340	.030	1.020
.360	.360	.640	.140	8.000	6.000	.833	1.911	1.090	1.800
7.280	1.690	-1.000							
1.680	2.030	2.290	1.130	1.790	.230	.290	.340	.010	1.060
.420	.380	.670	.140	9.000	9.000	.827	2.026	.936	1.580
7.570	1.690	-1.000							
1.936	2.190	2.380	1.090	1.680	.236	.251	.345	.047	.983
.361	.408	.597	.126	12.000	15.000	.834	2.183	1.152	1.989
-7.722	1.720	1.480							

QUEDIUS MESOMELINUS continued

1.407	2.004	2.190	1.430	1.690	14.220	.251	2.345	1.047	1.369
1.345	1.393	1.597	1.158	13.000	14.000	.904	2.126	1.069	1.924
6.259	1.799	1.290							
1.936	2.226	2.420	1.030	1.774	.236	.251	.345	.047	1.036
1.377	.393	.620	.158	13.000	12.000	.859	2.349	1.091	1.869
6.557	1.712	1.480							
-1.000	-1.000	2.290	-1.000	1.690	.251	-.298	-.345	-.047	-1.021
.377	.488	.581	.198	15.000	14.000	-1.000	-1.000	-1.000	-1.000
5.156	1.655	-1.000							
1.936	2.190	2.420	1.030	1.727	.251	.251	.345	.047	.969
1.361	.393	.612	.150	13.000	14.000	.884	2.349	1.121	1.957
6.593	1.786	1.480							
1.936	2.290	2.420	1.194	1.863	.236	.251	.345	.063	1.005
1.361	.393	.612	.150	-1.000	14.000	.859	2.345	1.063	1.959
6.700	1.854	1.462							
1.807	2.070	2.260	1.194	1.758	.236	.314	.314	.079	.969
1.361	.393	.565	.158	13.000	14.000	.873	1.892	1.026	1.827
6.259	1.777	1.323							
1.807	2.070	2.290	1.165	1.837	.314	.221	.377	.016	.973
1.361	.480	.597	.126	8.000	10.000	.872	2.150	.984	1.857
7.722	1.880	1.387							
1.645	1.807	2.832	.968	1.690	.283	.257	.314	.010	.911
1.393	.361	.597	.095	12.000	10.000	.911	2.099	.973	1.876
9.589	1.855	1.065							
1.471	2.194	2.387	1.065	1.774	.251	.251	.345	.310	1.021
1.361	.480	.565	.205	13.000	12.000	.852	2.241	1.055	1.832
4.981	1.737	1.516							
1.548	1.774	1.903	.903	1.664	.236	.257	.345	.010	.973
1.345	.393	.581	.150	8.000	7.000	.872	2.107	.930	1.591
6.487	1.710	1.194							
1.839	2.032	2.355	1.226	1.821	.236	.293	.330	.030	1.020
1.393	.345	.565	.182	10.000	11.000	.903	1.921	1.009	1.872
5.604	1.785	1.420							
1.471	2.097	2.323	1.226	1.790	.236	.298	.345	.063	1.036
1.393	.377	.659	.150	10.000	9.000	.832	1.894	1.045	1.806
6.906	1.727	1.387							
1.471	1.839	2.129	1.065	1.774	.236	.298	.330	.063	.973
1.361	.361	.565	1.142	11.000	13.000	.913	1.990	.945	1.972
6.452	1.823	1.258							
1.774	1.968	2.226	1.097	1.774	.236	.267	.314	.047	.942
1.361	.377	.565	.134	11.000	13.000	.901	2.029	1.000	1.883
7.029	1.883	1.258							
1.516	1.742	1.968	1.032	1.696	.220	.293	.330	.063	.973
1.377	.393	.597	.220	9.000	10.000	.870	1.907	.893	1.558
4.923	1.743	1.194							
1.678	1.936	2.194	1.161	1.806	.236	.283	.345	.010	1.099
1.345	.345	.644	.126	9.000	10.000	.855	1.889	.929	1.527
8.722	1.643	1.290							
1.936	2.194	2.484	1.323	1.821	.220	.267	.345	.010	1.063
1.345	.393	.565	.150	14.000	14.000	.852	1.877	1.063	1.988
5.700	1.681	1.516							
1.471	2.097	2.129	1.194	1.601	.236	.293	.314	.047	.911
1.361	.361	.534	.119	6.000	5.000	.892	1.783	1.169	2.054
7.655	1.757	1.290							
1.645	1.903	2.032	1.097	1.758	.267	.233	.345	.031	.942
1.424	.361	.550	1.126	10.000	10.000	.864	1.852	.936	1.926
7.476	1.866	1.194							
1.710	1.968	2.258	1.097	1.743	.236	.283	.345	.063	.973
1.377	.377	.554	.142	12.000	11.000	.858	2.158	.981	1.757
6.452	1.741	1.323							
1.839	2.037	2.323	1.161	1.806	.236	.298	.330	.063	1.021
1.393	.361	.597	.182	11.000	11.000	.877	2.000	1.018	1.801
5.610	1.769	1.355							
1.471	1.871	2.097	1.030	-1.000	.267	.236	.330	-.070	.879
1.377	.377	.565	.103	10.000	10.000	.914	2.036	-1.000	1.945
8.534	-1.000	1.226							
1.471	2.097	2.320	1.190	1.884	.314	.220	.393	.010	1.036
1.393	.393	.612	.157	9.000	11.000	.892	1.951	.993	1.875
6.599	1.819	1.320							
1.600	1.983	2.190	1.130	1.711	.251	.283	.330	.063	1.036
1.377	.361	.628	.110	9.000	6.000	.883	1.938	.982	1.622
9.418	1.852	1.260							
1.840	2.030	2.290	1.160	1.696	.314	.251	.345	.063	.998
1.408	.424	.644	.095	11.000	11.000	.906	1.974	1.085	1.921
10.084	1.770	1.290							
1.345	1.740	1.840	.968	1.680	.298	.251	.361	.047	.958
1.393	-1.000	.644	.110	11.000	11.000	.890	1.971	.921	1.616
8.709	1.754	1.030							
1.440	1.970	2.350	1.230	1.820	.314	.231	.361	.070	1.005
1.393	.345	.628	.134	12.000	12.000	.934	1.911	1.011	1.331
7.500	1.811	1.387							
1.645	1.807	2.065	1.065	1.650	-1.000	-1.000	-1.000	.063	.942
1.393	.345	.612	.119	15.000	12.000	.910	1.939	.997	1.746
7.316	1.752	1.226							
1.770	1.960	2.290	1.260	1.760	.251	.251	.345	.030	1.020
1.408	.377	.581	.119	11.000	9.000	.933	1.817	1.006	1.755
8.571	1.725	1.323							
1.650	1.870	2.090	1.030	1.710	.251	.251	.314	.063	.969
1.377	.377	.644	.110	8.000	9.000	.892	2.029	.965	1.668
8.991	1.729	1.230							
1.440	2.120	2.260	1.260	1.800	.236	.298	.361	.030	1.099
1.393	.361	.659	.126	9.000	9.000	.915	1.794	1.786	1.785
8.722	.988	1.320							
1.940	2.070	2.420	1.320	1.710	.251	.298	.330	.010	1.021
1.377	.345	.628	.157	12.000	11.000	.937	1.833	1.135	1.901
6.503	1.675	1.464							
1.810	2.030	2.390	1.190	1.760	.188	.298	.330	.020	1.099
1.377	.345	.691	.157	12.000	11.000	.892	2.008	1.028	1.647
7.000	1.601	1.320							
1.680	1.840	2.000	1.097	1.740	.267	.283	.424	.094	.973
1.393	.393	.581	.141	14.000	11.000	.913	1.823	.966	1.727
6.901	1.788	1.230							
1.710	1.940	2.130	1.070	1.760	.283	.251	.345	.063	.942
1.393	.377	.628	.103	8.000	9.000	.881	1.991	.972	1.815
-9.146	1.668	1.190							

GROUP 1 (CONTAINING 13 SETS OF OBSERVATIONS) Extra-european *Quedius mesomelinus*

VARIABLE	MEAN	STANDARD ERROR	VARIANCE	STANDARD DEVIATION	COEFF. OF VARIATION	MINIMUM	MAXIMUM	RANGE	SAMPLE SIZE
1	1.7315	.0351	.0169	.1300	7.5172	1.4509	1.8709	.4200	13
2	1.9246	.0357	.0166	.1288	6.6331	1.6713	2.1810	.5097	13
3	1.1462	.0170	.0030	.0545	4.7563	1.0403	2.2600	1.2197	13
4	1.1033	.0170	.0030	.0545	4.7563	1.0300	1.8330	.8030	13
5	1.6833	.0170	.0027	.0516	3.0642	1.5900	1.7800	.1900	12
6	.2308	.0133	.0001	.0110	4.8197	.2200	.2500	.0300	12
7	.2583	.0133	.0001	.0110	4.8197	.2300	.2600	.0300	12
8	.3025	.0141	.0002	.0142	4.7316	.2800	.3300	.0500	12
9	.0425	.0033	.0004	.0131	3.0088	.0100	.0800	.0700	12
10	.6667	.0133	.0005	.0227	3.3300	.9500	1.5200	.5700	12
11	.3808	.0133	.0004	.0212	5.5101	.3400	.4200	.0800	12
12	.1625	.0133	.0005	.0227	14.81	.3400	.4100	.0700	12
13	.5917	.0133	.0005	.0217	3.6330	.5500	.6200	.0700	12
14	.1332	.0133	.0011	.0329	2.6200	.6400	1.0000	.3600	12
15	11.9167	.7113	5.9015	2.4293	20.2332	8.0000	15.0000	7.0000	12
16	11.8333	.7170	6.9370	2.5979	22.2170	8.0000	15.0000	7.0000	12
17	.6990	.0357	.0004	.0182	2.1305	.6630	.9220	.2590	13
18	1.9446	.0357	.0110	.1376	5.3321	1.7809	2.1810	.4000	13
19	1.0230	.0241	.0079	.0832	3.1574	.8730	1.1310	.2580	12
20	.7747	.0170	.0064	.1282	7.2226	1.5300	1.9500	.4200	12
21	7.3503	.5715	3.3187	1.8216	25.9039	5.1100	11.8750	6.7650	12
22	1.7333	.0170	.0037	.0607	3.4893	1.6400	1.8310	.1910	12
23	TOO FEW OBSERVATIONS ON THIS VARIABLE								

QUEDIUS MESOMELINUS continued

1.748	1.903	2.097	1.097	1.730	.330	.257	.361	.063	.958
.345	.424	.628	.110	8.000	9.000	.914	1.912	1.006	1.816
8.709	1.806	1.260							
1.960	2.260	2.516	1.290	1.790	.298	.251	.361	.47	1.005
.424	.408	.628	.110	12.000	12.000	.857	1.950	1.095	1.950
9.136	1.781	1.548							
1.870	2.130	1.720	1.190	1.740	.314	.220	.345	.063	.973
.393	.408	.644	.126	14.000	13.000	.878	2.034	1.175	1.922
7.722	1.788	1.398							
1.810	2.030	2.130	1.161	1.730	.314	.220	.345	.063	.973
.393	.408	.659	.094	11.000	8.000	.892	1.835	1.079	1.969
10.521	1.749	1.320							
1.940	2.190	2.420	1.260	1.710	.345	.220	.361	-1.000	.942
.393	.377	.644	.095	10.000	12.000	.886	1.921	1.135	2.059
9.916	1.815	1.398							
1.770	2.800	2.230	1.130	1.696	.298	.236	.330	.063	.973
.377	.393	.659	.103	7.000	6.000	.885	1.973	1.144	1.819
9.447	1.743	1.323							

GROUP 1 (CONTAINING 124 SETS OF OBSERVATIONS) European Quedius mesomelinus

VARIABLE	MEAN	STANDARD ERROR	VARIANCE	STANDARD DEVIATION	COEFF. OF VARIATION	MINIMUM	MAXIMUM	RANGE	SAMPLE SIZE
1	1.7244	.0119	.0173	.1317	7.6351	1.4000	1.9800	.5800	122
2	1.9531	.0134	.0221	.1485	7.6305	1.6000	2.2900	.6900	122
3	1.7002	.0141	.0274	.1654	7.9435	1.7700	2.5100	.7400	124
4	1.1111	.0139	.0099	.0997	8.9370	.9000	1.3300	.4300	123
5	1.6711	.0131	.0140	.1184	7.2215	1.3000	1.9400	.6400	120
6	1.2444	.0135	.0100	.1000	8.3377	1.0000	1.3500	.3500	120
7	1.2777	.0131	.0095	.0970	9.0700	.9200	1.3700	.4500	119
8	1.2771	.0143	.0120	.1098	8.2184	.9500	1.7900	.8400	120
9	1.3322	.0143	.0120	.1098	9.3300	.9100	1.7900	.8800	121
10	1.3849	.0141	.0121	.1100	8.1833	.8700	1.7900	.9200	121
11	1.3877	.0139	.0106	.1030	6.1373	.8500	1.4500	.6000	122
12	1.3300	.0133	.0090	.0944	8.5663	.8300	1.4500	.6200	119
13	1.3300	.0133	.0090	.0944	8.3784	.8000	1.4500	.6500	122
14	1.1395	.0134	.0086	.0927	8.7441	.8700	1.2200	.3500	122
15	1.2333	.0133	.0090	.0944	7.4556	6.0000	12.0000	12.0000	73
16	1.4384	.0139	.0175	.1324	21.7314	5.0000	16.0000	11.0000	73
17	1.8333	.0127	.0309	.1760	3.3333	.7270	9.4500	8.7200	122
18	1.9333	.0135	.0133	.1155	3.0433	1.6420	2.3400	.7000	123
19	1.3122	.0131	.0127	.1124	11.6193	.8400	2.7800	1.9400	118
20	1.7333	.0131	.0107	.1033	3.2471	1.1610	2.0500	.8900	120
21	1.2818	.0115	.0121	.1094	18.4369	4.4230	11.1800	6.7600	122
22	1.7041	.0139	.0139	.1178	9.6119	.9500	1.9800	.9300	120
23	1.3133	.0132	.0125	.1115	3.5217	1.0300	1.5400	.5100	54

GROUP 1 (CONTAINING 137 SETS OF OBSERVATIONS) All Quedius mesomelinus

VARIABLE	MEAN	STANDARD ERROR	VARIANCE	STANDARD DEVIATION	COEFF. OF VARIATION	MINIMUM	MAXIMUM	RANGE	SAMPLE SIZE
1	1.7251	.0113	.0172	.1310	7.5359	1.4000	1.9800	.5800	135
2	1.9435	.0123	.0213	.1465	7.5170	1.6000	2.2900	.6900	135
3	1.7133	.0141	.0274	.1654	7.9497	1.7700	2.5100	.7400	137
4	1.1177	.0139	.0099	.0997	8.9449	.9000	1.3300	.4300	136
5	1.6732	.0131	.0140	.1184	8.7127	1.3000	1.9400	.6400	132
6	1.2414	.0135	.0100	.1000	11.0330	1.0000	1.3500	.3500	132
7	1.2737	.0131	.0095	.0970	9.0747	.9200	1.3700	.4500	131
8	1.2771	.0143	.0120	.1098	8.2148	.9500	1.7900	.8400	132
9	1.3322	.0143	.0120	.1098	9.2137	.9100	1.7900	.8800	133
10	1.3849	.0141	.0121	.1100	8.4713	.8700	1.6900	.8200	133
11	1.3877	.0139	.0106	.1030	6.1138	.8300	1.4500	.6200	134
12	1.3300	.0133	.0090	.0944	6.5276	.8000	1.4500	.6500	131
13	1.3300	.0133	.0090	.0944	6.5276	.8000	1.4500	.6500	131
14	1.1395	.0134	.0086	.0927	8.7441	.8700	1.2200	.3500	134
15	1.2333	.0133	.0090	.0944	13.2404	.6800	2.2000	1.5200	90
16	1.4384	.0139	.0175	.1324	21.7163	6.0000	16.0000	12.0000	91
17	1.8333	.0127	.0309	.1760	3.3333	.7270	9.4500	8.7200	135
18	1.9333	.0135	.0133	.1155	3.0433	1.6420	2.3400	.7000	136
19	1.3122	.0131	.0127	.1124	13.3843	.8400	1.7800	.9400	130
20	1.7333	.0131	.0107	.1033	3.4469	1.1610	2.0500	.8900	132
21	1.2818	.0115	.0121	.1094	13.2889	4.4230	11.6700	7.2500	134
22	1.7041	.0139	.0139	.1178	9.6317	.9500	1.9800	.9300	132
23	1.3133	.0132	.0125	.1115	3.5217	1.0300	1.5400	.5100	54

GROUP 2 (CONTAINING 11 SETS OF OBSERVATIONS) British Quedius maurus

VARIABLE	MEAN	STANDARD ERROR	VARIANCE	STANDARD DEVIATION	COEFF. OF VARIATION	MINIMUM	MAXIMUM	RANGE	SAMPLE SIZE
1	1.4891	.0278	.0185	.0924	6.2020	1.3500	1.6400	.2900	11
2	1.7027	.0379	.0158	.1255	7.3732	1.5800	1.8700	.2900	11
3	1.9682	.0407	.0183	.1351	6.8650	1.7700	2.1900	.4200	11
4	1.0175	.0226	.0056	.0749	7.3623	.9000	1.1300	.2300	11
5	1.4860	.0128	.0016	.0403	2.7141	1.4400	1.5700	.1300	10
6	.3200	.0193	.0007	.0262	8.2021	.2600	.3400	.0800	10
7	.2300	.0170	.0005	.0221	9.6134	.2000	.2700	.0700	10
8	.0382	.0035	.0001	.0117	30.5839	.0100	.0600	.0500	11
9	.9109	.0174	.0006	.0247	2.7094	.8600	.9400	.0800	11
10	.2955	.0145	.0002	.0151	5.1025	.2700	.3100	.0400	11
11	.2473	.0043	.0002	.0142	5.7452	.2200	.2800	.0600	11
12	.5107	.0038	.0001	.0326	6.3922	.4700	.5600	.0900	11
13	.2318	.0129	.0018	.0429	13.4555	.1800	.2900	.1100	11
14	TOO FEW OBSERVATIONS CN THIS VARIABLE								
15	TOO FEW OBSERVATIONS CN THIS VARIABLE								
16	.8743	.0082	.0007	.0271	3.0997	.8210	.9180	.0970	11
17	1.9382	.0349	.0133	.1155	5.9610	1.7430	2.1040	.3610	11
18	1.0001	.0130	.0022	.0474	4.7358	.9380	1.0800	.1420	10
19	1.6335	.0231	.0073	.0834	5.1062	1.5330	1.6820	.1490	11
20	4.0576	.2313	.5883	.7670	18.9331	2.9660	5.1110	2.1450	11
21	1.6269	.0102	.0010	.0323	1.9859	1.5879	1.6740	.0870	10
22	TOO FEW OBSERVATIONS CN THIS VARIABLE								

GROUP 2 (CONTAINING 21 SETS OF OBSERVATIONS) European Quedius maurus

VARIABLE	MEAN	STANDARD ERROR	VARIANCE	STANDARD DEVIATION	COEFF. OF VARIATION	MINIMUM	MAXIMUM	RANGE	SAMPLE SIZE
1	1.4851	.0132	.0078	.0881	5.9327	1.3230	1.6400	.3170	21
2	1.6779	.0255	.0136	.1160	6.9556	1.4840	1.8700	.3860	21
3	1.9459	.0238	.0174	.1318	6.7768	1.6450	2.1900	.5450	21
4	1.0031	.0134	.0057	.0753	7.5080	.9000	1.1300	.2300	21
5	1.4369	.0115	.0022	.0469	3.1550	1.4130	1.5700	.1570	20
6	.3186	.0143	.0005	.0220	6.4909	.2600	.3450	.0850	20
7	.2297	.0118	.0003	.0170	7.3945	.2000	.2700	.0700	20
8	.0735	.0033	.0004	.0115	14.5304	.0100	.0700	.0600	21
9	.9056	.0231	.0124	.1115	3.2683	.8480	.9420	.0940	21
10	.2968	.0117	.0003	.0169	3.7083	.2670	.3140	.0470	21
11	.2514	.0015	.0003	.0165	6.5565	.2200	.2830	.0630	21
12	.5008	.0171	.0010	.0322	6.4225	.4400	.5600	.1200	21
13	.2310	.0133	.0015	.0381	10.4388	.1800	.3140	.1340	21
14	9.1003	.8003	2.7667	1.6633	18.2784	7.0000	11.0000	4.0000	10
15	8.6000	.5377	1.7111	1.6465	13.1459	5.0000	11.0000	6.0000	10
16	.8860	.0333	.0006	.0241	2.7233	.8210	.9200	.0990	21
17	1.9456	.0228	.0109	.1045	5.3701	1.7430	2.1370	.3940	21
18	1.9978	.0139	.0019	.0441	4.4239	.9360	1.0860	.1500	20
19	1.6356	.0167	.0059	.0767	4.6368	1.4780	1.8020	.3240	21
20	3.9890	.1426	.4273	.6537	18.3876	2.9660	5.1110	2.1450	21
21	1.6401	.0101	.0020	.0451	2.7517	1.5790	1.7630	.1840	20
22	1.2020	.0733	.0377	.1941	16.1443	1.0320	1.6100	.5780	7

GROUP 1 (CONTAINING 29 SETS OF OBSERVATIONS) skoraszewskyi

VARIABLE	MEAN	STANDARD ERROR	VARIANCE	STANDARD DEVIATION	COEFF. OF VARIATION	MINIMUM	MAXIMUM	RANGE	SAMPLE SIZE
1	1.7237	.0211	.0129	.1134	6.5786	1.4620	1.8710	.4090	29
2	1.9341	.0230	.0167	.1293	6.6832	1.7100	2.1940	.4840	29
3	1.1734	.0203	.0121	.1451	6.8864	1.9000	2.4200	.5200	29
4	1.1107	.0144	.0060	.0774	6.9664	1.9360	1.2900	.3540	29
5	1.8073	.0170	.0084	.0918	5.0788	1.6600	2.0000	.3400	29
6	1.3161	.0053	.0011	.0337	10.6680	.2800	.3530	.1130	29
7	1.3406	.0144	.0035	.0211	6.7890	.3100	.3930	.0830	29
8	1.0840	.0316	.0290	.1702	266.1209	.0100	.9400	.9300	29
9	1.0865	.0103	.0030	.0552	3.0828	.9730	1.1930	.2200	29
10	1.3806	.0034	.0003	.0185	4.8675	.3400	.4080	.0680	29
11	1.3743	.0157	.0116	.0339	3.2590	.3400	.4400	.1000	29
12	1.6638	.0174	.0116	.0339	6.0047	.5970	.7650	.1720	29
13	1.1452	.0039	.0004	.0210	14.4437	.1110	.2040	.0930	29
14	1.3704	.0304	3.7037	1.9245	20.5382	6.0000	14.0000	8.0000	29
15	1.6296	.0342	3.7806	1.9444	20.1917	6.0000	14.0000	8.0000	29
16	1.8919	.0063	.0112	.0342	3.8237	.8530	1.0000	.1470	29
17	1.9604	.0274	.0251	.1586	6.0887	1.6380	2.2980	.6520	29
18	1.9348	.0111	.0036	.0597	6.2537	.8140	1.0470	.2330	29
19	1.9371	.0158	.0073	.0332	5.3695	1.3790	1.7570	.3780	29
20	1.6999	.0133	.0041	.0370	12.9697	1.1670	1.6220	.4550	29
21	1.6649	.0129	.0048	.0691	4.1482	1.5370	1.8480	.3110	29
22	1.3036	.0220	.0092	.0961	7.3702	1.1300	1.4190	.2890	29

GROUP 1 (CONTAINING 3 SETS OF OBSERVATIONS) silensis

VARIABLE	MEAN	STANDARD ERROR	VARIANCE	STANDARD DEVIATION	COEFF. OF VARIATION	MINIMUM	MAXIMUM	RANGE	SAMPLE SIZE
1	1.7633	.0107	.0003	.0185	1.0477	1.7420	1.7740	.0320	3
2	1.9677	.0323	.0031	.0560	2.8462	1.9030	2.0000	.0970	3
3	1.1933	.0431	.0072	.0330	3.3770	2.1300	2.2900	.1600	3
4	1.1190	.0113	.0025	.0191	1.7026	1.0970	1.1300	.0330	3
5	1.7907	.0474	.0067	.0820	4.5811	1.7300	1.8840	.1540	3
6	1.3130	.0138	.0006	.0239	7.4908	.2980	.3450	.0470	3
7	1.2823	.0313	.0020	.0511	19.2223	.2510	.3450	.0940	3
8	1.3537	.0137	.0003	.0165	3.1945	.5450	.3770	.6320	3
9	1.0467	.0195	.0003	.0165	3.3623	.0300	.0630	.0330	3
10	1.9470	.0133	.0006	.0239	2.7233	.9260	.9730	.0470	3
11	1.4130	.0260	.0020	.0450	10.7478	.3930	.4710	.0780	3
12	1.3930	.0000	.0000	.0000	.3930	.3930	.3930	.0000	3
13	1.6230	.0138	.0006	.0239	3.8356	.5970	.6440	.0470	3
14	1.1107	.0113	.0004	.0206	18.6139	.0950	.1340	.0390	3
15	1.0000	1.5275	.7000	26.4575	26.4575	8.0000	13.0000	5.0000	3
16	1.3333	1.4333	.6333	25.1666	26.9637	7.0000	12.0000	5.0000	3
17	1.8963	.0193	.0003	.0162	1.8035	.8870	.9150	.0280	3
18	1.9617	.0136	.0022	.0182	5.6196	1.8850	2.0880	.2030	3
19	1.9860	.0244	.0017	.0417	4.2318	.9420	1.8250	.8830	3
20	1.8627	.0277	.0023	.0480	2.5760	1.8230	1.9160	.0930	3
21	1.7718	.0713	.1682	1.2971	1.8783	7.2610	9.7470	2.4860	3
22	1.8900	.0130	.0016	.0393	2.1085	1.8660	1.9360	.0700	3
23	1.2260	.0320	.0031	.0554	4.5209	1.1940	1.2900	.0960	3