

THE BIOLOGY
OF
THE COLEOPTERA



R. A. CROWSON

**The Biology
of the Coleoptera**

This page intentionally left blank

The Biology of the Coleoptera

R. A. CROWSON
University of Glasgow
Glasgow, Scotland

1981



ACADEMIC PRESS

Harcourt Brace Jovanovich, Publishers

LONDON ORLANDO NEW YORK SAN DIEGO
AUSTIN BOSTON TOKYO SYDNEY TORONTO

Academic Press Inc. (London) Ltd
24-28 Oval Road
London NW1

US edition published by
Academic Press Inc.
Orlando, Florida, 32887

Copyright © 1981 by Academic Press Inc. (London) Ltd

Second printing, 1986

All Rights Reserved

No part of this book may be reproduced in any form,
by photostat, microfilm or any other means,
without written permission from the publishers

British Library Cataloguing in Publication Data

Crowson, Roy Albert
The biology of the Coleoptera
1. Beetles
I. Title
595.7'6 QL573 77-71815

ISBN 0-12-196050-1

Printed by W. & G. Baird Ltd.
at The Greystone Press, Antrim, N. Ireland.

I followed after the living thing, I went upon the broadest and narrowest paths that I might know its nature.

F. NIETZSCHE, "Also sprach Zarathustra", 1883,
translated by A. Tille and M. M. Bozman

. . . this is practically the claim of the egoism which thinks that self-assertion can obtain knowledge. A beetle may or may not be inferior to a man—the matter awaits demonstration; but if he were inferior to a man by 10,000 fathoms, the fact remains that there is probably a beetle view of things of which a man is entirely ignorant.

G. K. CHESTERTON, "On Humility",
in "The Defendant", 1901

This page intentionally left blank

Foreword

In number of described species beetles represent the largest group of organisms at the order level. They also show exceptionally diverse adaptations to very different environments and habits, exploit the most varied types of food, and use all possible methods of locomotion. Their role in the operation of ecosystems, particularly on land, should never be underestimated.

There are species that can consume nearly every part of most known types of green plants, others specialising in fungi, decaying animal or vegetable matter, predators on very diverse types of invertebrates, commensals or parasites of social insects, ectoparasites of vertebrates, and parasitoids of other insects.

The major ecological impacts of beetles, all over the globe, result from their effects on green plants, their contribution to the breakdown of plant and animal debris and the formation of soil, and their predatory activities; many species have economic importance for man, often injurious but sometimes beneficial. We may number beetles among our friends as well as our foes, and in either case they deserve and receive scientific study.

Many species of the order are markedly stenobiotic, with very special ecological requirements for their continued existence; such species can be sensitive indicators of ecological conditions and of the effect on ecosystems of human activities. Beetles also provide suitable material for all types of comparative biology. They also offer a classic example of evolutionary diversification based on a fundamentally uniform ground plant, affecting every type of characteristic which can be studied by the most modern research techniques. As Dr Crowson writes, "the Coleoptera provide excellent illustrations and test cases for almost every general evolutionary principle, and future study of the group may well lead to the formulation of new generalisations" (p. 691). The Coleoptera may rival or even surpass the Vertebrata in this respect.

In the title of Dr Crowson's book, the word "Biology" is used in the modern sense, implying the totality of biological knowledge of the group concerned, rather than meaning merely the description of the modes of life of the species; this book summarises the results of the study of beetles using the most modern experimental techniques.

To prepare a modern manual dealing with Coleoptera in relation to all types of biological problems requires an author with an exceptional devotion to the group, characterised by Dr Crowson as one of those "eccentrics who would wish to devote their entire lives to the study of beetles" (p. 689), and in this category Dr Crowson himself certainly belongs; he is indeed a world authority

on the systematics of beetles. A revised version of his classification of the order forms a necessary and useful appendix to this book. Dr Crowson has been at pains to indicate clearly, for the benefit of non-systematists, the systematic position of all the genera and species referred to in this book. Revisions of his own system on the basis of further knowledge may be exemplified by the Cicindelidae, treated as a subfamily of Carabidae in his 1955 book, but here restored to full family status.

This book summarises an immense literature in many languages, covering all branches of modern biology, but is no mere compilation; the ordering and interpretation of the evidence reflects the individuality and rich experience of the author. In spite of the very little explicit attention in it to the practical economic problems of coleopterology, the book should prove as valuable to applied entomologists as to "pure" scientists in any field who may be concerned with beetles. This book should be read and enjoyed by readers with many types of interest, as it has been in the proof stage by me.

Moscow
January 1981

M. GHILAROV

Preface

To deal with so vast a group as the Coleoptera in respect of all branches of modern biology is doubtless an over-ambitious aim for any single author; it is inevitable that my attempt to do so will not satisfy specialists in their own particular fields. I hope, however, that such specialists, once they have overcome their initial dissatisfaction, may gain from this book by coming to see their particular research interests in wider contexts, and perhaps even by picking up ideas which might suggest new and fruitful directions for their investigations. At all points I have tried not merely to summarise available knowledge but also to draw attention to serious gaps in it.

The number of previous authors, living and dead, to whom I am indebted for facts, ideas and illustrations is very great, and my gratitude to all of them is deep and sincere. There must be almost as many researchers whose useful original contributions to subjects treated in this book I have unfairly overlooked and ignored in it; to them, the only excuse I can plead is the general one of human weakness and fallibility inevitably manifest in myself.

For the preparation of this book, generous facilities have been provided over several years in the Zoology Department of Glasgow University, by courtesy of Professor D. R. Newth and Professor K. Vickerman, to both of whom my best thanks are due. I have also been greatly helped by the patient editorial work of Mrs D. Sharp, to whom such measures of orthographic consistency as the book possesses are largely due.

December 1980

R. A. CROWSON

This page intentionally left blank

Contents

Foreword	vii
Preface	ix
<i>Chapter 1</i> Introduction: The Study of Beetles	1
<i>Chapter 2</i> Some Skeletal Peculiarities of the Adults	15
<i>Chapter 3</i> Internal Structures of the Adults	76
<i>Chapter 4</i> Some Structural Features of Larvae and Pupae	119
<i>Chapter 5</i> Food, Digestion and the Alimentary Canal	160
<i>Chapter 6</i> Blood, Osmoregulation, Reserves, Excretion and Endocrine Organs	184
<i>Chapter 7</i> Locomotion, Respiration and Energetics	204
<i>Chapter 8</i> The Senses	242
<i>Chapter 9</i> Cuticular Properties, Appearance, Colour and Luminosity	292
<i>Chapter 10</i> Adult and Larval Behaviour	322
<i>Chapter 11</i> Development and Life-cycles	358
<i>Chapter 12</i> Cytology and Genetics	397
<i>Chapter 13</i> Water Beetles	429
<i>Chapter 14</i> Special Habitats	457
<i>Chapter 15</i> Predation and Defence	482
<i>Chapter 16</i> Symbiotic and Parasitic Relations	519
<i>Chapter 17</i> An Ecological Triangle: Beetles, Fungi and Trees	559
<i>Chapter 18</i> Herbivorous Beetles	584
<i>Chapter 19</i> Geographical Distribution and Conservation: Beetles as Ecological Indicators	619
<i>Chapter 20</i> Evolutionary History of Beetles	658

<i>Chapter 21</i>	Epilogue	689
Bibliography		699
Taxonomic Index		747
Subject Index		773

Chapter 1

Introduction:

The Study of Beetles

Whenever I hear of the capture of rare beetles, I feel like an old warhorse at the sound of a trumpet.

C. Darwin

The beetles are at once absolutely typical of, and unique among, the Insecta, a paradox of a kind which, though familiar to any practising systematist, is a constant stumbling block to laboratory experimentalists of the modern school. There is probably no single elementary property or condition which is common to all Coleoptera and to no other insects, and no single proposition which can be made of all other insects which does not apply to at least some Coleoptera. The beetles, nevertheless, form an isolated and well-characterised taxon, correctly recognised and named by Aristotle as far back as the fourth century B.C. (translation, Wentworth Thompson, 1910).

Human interest in Coleoptera can be traced considerably further back than that in history and prehistory. The sacred scarabs of ancient Egypt (Fig. 1) were venerated at least as far back as 2000 B.C., and the examples of some of the most primitive recent human tribes suggest that beetle larvae may have been a significant element in the diets of many palaeolithic men. The luminosity of fireflies, the poisonous properties of certain Chrysomelidae, and the brilliant metallic colours of some large Buprestidae, have all attracted the attention of primitive peoples in many parts of the world, and the medicinal properties of the cantharidin of the Meloidae were known in classical antiquity, as were the depredations of beetles in food stores (Virgil's "Georgics", Book I).

In more modern times, Albrecht Durer's celebrated representation (Fig. 2) of a stag beetle (*Lucanus cervus*) is probably the oldest European picture of a beetle which can be reliably identified to the species. Shakespeare's 'shard-borne beetle' was probably a *Geotrupes* species, and records from his day show that, on the long voyages of Elizabethan mariners, food stores were liable to be damaged by "stored product" beetles, generally known as "Weevils".

Beetles probably began to be systematically collected and compared at about the time of John Ray (1627–1705) and J. J. Swammerdam, leading to the appearance of the first formal published system of the group, that of Linnaeus, who named a considerable number of the commoner and more conspicuous European beetles in his “*Systema Naturae*” of 1758. The labours of his successors, notably of Fabricius, Latreille, Erichson and Lacordaire, transformed the admittedly artificial Linnaean system, providing the essential bases for modern classifications, which have advanced steadily in the direction

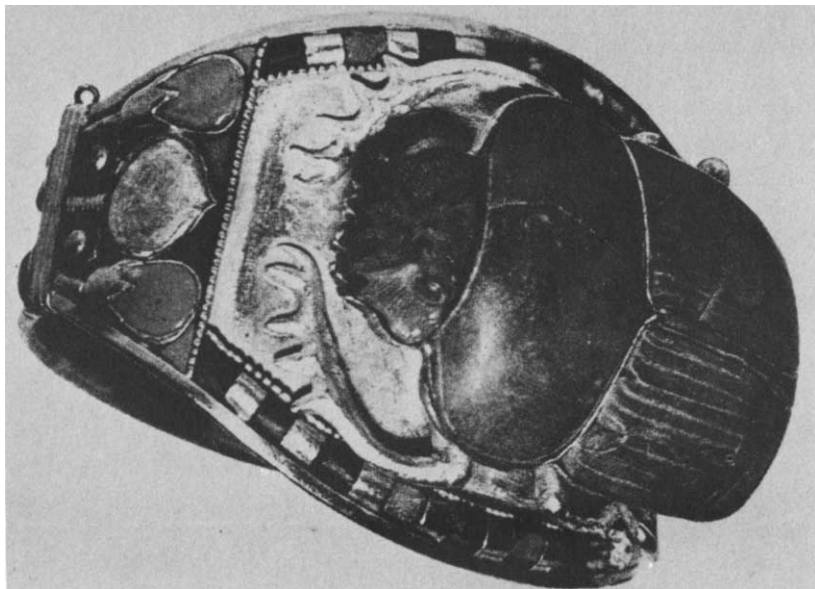


FIG. 1. Egyptian Scarab Brooch, c. 1000 B.C.

of a phylogenetic system—the ideal set before us by Charles Darwin, who, for all his life-long interest in beetles, made no attempts himself to improve the classification of the group. With well over a quarter of a million species now named, described and catalogued, the Coleoptera take a pre-eminent position among the orders of insects, and indeed among all animal groups of comparable status. The quip of T. H. Huxley, that one thing we know about a divine Creator, supposing one to exist, is that he has a particular interest in Coleoptera, still has force.

The economic importance of various species of beetles was well known by the time of Gilbert White, who in his “*Natural History of Selborne*” (1784), noted the depredations of flea-beetles (*Phyllotreta* spp.) in the turnip fields which the “agricultural revolution” of the eighteenth century had brought to the Selborne area. Curtis’s “*Farm Insects*” (1841–57) included remarkably

accurate and detailed accounts of a considerable number of species of Coleoptera. It is now realised that, against the more or less injurious activities of many Curculionidae, Chrysomelidae, Scarabaeidae, Tenebrionidae, etc., there can be set the value of Coccinellidae as destroyers of injurious Homoptera, of Carabidae and Staphylinidae as predators of lepidopterous and dipterous pests, of some Chrysomelidae as devourers of injurious plants, and so on.

The number of modern works dealing with beetles in relation to agriculture is very great; perhaps the most encyclopaedic of them is that of Balachowsky



FIG. 2. Stag Beetle: water colour by Albrecht Durer (1505.)

(1962–63), which, however, deals only with agriculture of Europe and the Mediterranean region. Comparable data for the USA are subsumed in Metcalf and Flint (1962), and briefer information on injurious Coleoptera from a number of tropical regions, mainly in the Old World, is given by Evans (1952).

The literature on beetles in relation to trees and timber is also very extensive. In this domain, perhaps the most comprehensive work is the German one of Escherich (1927) dealing primarily with European species. Beeson (1941) provides an encyclopaedia of the Indian ones (following an interesting earlier work of Stebbing, 1914), and Froggatt's review of Australian forest Coleoptera (1923) still has much of interest. For the North American fauna, Chamberlain (1939) reviewed the bark and timber beetles. A world-wide review of the Platypodinae (V10) by Schedl (1972) provides much biological data, as does the same author on African Scolytinae (1959–62).

An important category among insect pests is formed by the species infesting man-made stores of many types of more or less dry organic materials, mainly but not exclusively used as human or animal foods. Among these "stored product insects" a centrally important place is occupied by the beetles, and very largely by cryptonephric species of Bostrychiformia and Cucujiformia. Clearly, these beetles are in some way pre-adapted to this type of habitat. One of their pre-adaptive features is surely the water-economising power conferred by cryptonephridism; others are probably the unusually strong and protective exoskeleton, and the long lives of many of the adults. A firm outer armour probably helps the beetles to survive the violent mechanical disturbances to which such stores are often liable, and their long lives may enable the adults to survive over extended periods while the store may lie empty.

The main beetle pests of stored products belong to the families Dermestidae (P3), Bostrychidae (Q1), Anobiidae (including Ptininae; Q2), Trogossitidae (R4), Cleridae (R6), Nitidulidae (T1), Cucujidae-Laemophloeinae (T8), Silvanidae (T11), Tenebrionidae (T56), Bruchidae (U4), Anthribidae (U2), and Curculionidae (including Scolytinae: V10); in addition to these, a number of other families, such as Cryptophagidae (T13), Cerylonidae (T21), Latrhiidae (T28) and Mycetophagidae (T32) may be represented where conditions are damp enough to permit the growth of moulds. A number of extensive works have been published on stored product beetles, the more important of them including those of Hinton (1945), Lepesme (1944), and Aitken (1975). As noted by the last author, most of these species have achieved an almost cosmopolitan distribution.

Beetles may also be destructive to timber in buildings, packing cases, furniture etc. the main groups concerned being Cerambycidae (U2, e.g. *Hylotrupes*), Lyctinae (Q1), and Anobiidae (Q2). In *Hylotrupes* and several of the Anobiidae the larvae can develop in seasoned and rather dry wood, and indoor infestations may be self-perpetuating and cumulative, hence highly damaging.

The use of species of Coleoptera as "material" for diverse laboratory and experimental investigations is long established. There are three considerations which, singly or conjointly, are liable to influence the experimentalist's selection of a species on which to experiment: large size, ready availability and culturability, and manifestation to an unusual degree of the function or phenomenon in which he is interested. Each of these criteria would lead him to select a species which is not really typical of the order Coleoptera. As is now well known, the approximate constancy of cell sizes, and the effects of changing surface to volume ratios, imply that a large species cannot be an accurate scale model of a small one. The more readily available and culturable beetles belong to the previously mentioned "stored product" species, which must be in some degree physiologically and behaviourally

aberrant in relation to their "wild" relatives. A species manifesting a particular function to an exceptional degree is likely to be, by that very token, abnormal in respect of that function. Thus the experimental data on Coleoptera which are available in the published literature, valuable as they are, may tend to give distorted impressions of the order as a whole. I fear that there is very little hope that future experimentalists will redress the balance by concentrating their studies on species which are small, "wild" and not manifesting the desired phenomena to exceptional degrees.

The present work does not deal specifically with the classification of Coleoptera, though a conspectus of the author's system, explained in detail in other works (Crowson, 1955, 1960, 1967, 1971, 1972, 1973) is appended at the end, and taxa mentioned in the text are referred to it by appropriate letters and numbers. When discussing particular phenomena and characteristics, specific genera to which published observations refer are usually named in the text. It is not to be expected that the system here used is a perfectly phylogenetic one in the sense of Hennig (1966) or Crowson (1971), but it is my hope that it approaches this ideal more closely than any other yet proposed.

Most systematists have included Coleoptera in a group Endopterygota, including all those orders in which development is by way of a "complete metamorphosis" involving several larval instars during which no progress towards the adult characteristics is manifested externally, followed by a single non-feeding pupal instar, which gives rise directly to the adult. This mode of development links the beetles with Hymenoptera, Diptera, Lepidoptera and a number of smaller orders. There was a rival theory, advocated particularly in the works of the German palaeontologist Handlirsch, that the Endopterygota were an unnatural, polyphyletic group, and that the true affinity of the Coleoptera was towards the orthopteroid orders, and particularly towards the Dictyoptera. Practically no evidence, beyond superficial similarities of beetles to cockroaches, has been produced in favour of this hypothesis, except perhaps for some doubtfully interpreted Palaeozoic fossils (e.g. the Protelytroptera, now suspected of being precursors of Dermaptera), and recent biochemical evidence has supported the theory of the unity of Endopterygota.

If the beetles truly belong to Endopterygota, there remains to be established their precise relations to other orders of the group. A major division is constituted by the orders of the so-called "Panorpoid complex", including Mecoptera, Siphonaptera, Diptera, Trichoptera, Zeugloptera and Lepidoptera; there is little or no evidence for a direct affinity of Coleoptera to any of the orders in this group. Outside the Panorpoid complex as usually constituted there remain the Hymenoptera, Raphidioptera, Neuroptera and Megaloptera, as well as the beetles. There are no significant indicators of a particular affinity of beetles to Hymenoptera, and recent evidence tends to strengthen the view that the latter group belongs with the Panorpoid complex. Most modern

authorities (e.g. Hennig, 1969) would consider that the beetles are related nearly equally to the Neuroptera and Megaloptera, with the position of the Raphidioptera rather more problematic. Neither Megaloptera nor Neuroptera, as now characterised, could, however, include the ancestors of Coleoptera whose larvae could hardly have had the specialised mouthparts of the Neuroptera or the aquatic adaptations of the Megaloptera.

In search for useful biological generalisations, analogies are perhaps even more useful than homologies; the distinction between homologies and analogies, fundamental as it is for systematists and phylogenists, is apt to seem rather academic to physiologists, ecologists, ethologists, etc. The closest analogies to beetles are generally to be found in other orders of the Insecta, but some may be traced even in so systematically remote a group as the Vertebrata. One vertebrate group, the reptilian Chelonia, is particularly interesting from this point of view. In it we find an overall body form which is very similar to that of many Polyphaga, such as Histeridae, Limnichidae, Chrysomelidae-Chrysomelinae, Cerylonidae-Murmidiinae, etc., with a hard outer shell and more or less retractable head and appendages. Like the beetles, the Chelonia are notable for their adult longevity, for their long-lasting evolutionary success, and for adaptability in respect of foods. Even more than the Coleoptera, the Chelonia have successfully colonised the water, though they have been less successful in adapting the dry desert-type habitats. A most interesting parallel is to be seen in the fact that a major division of existing Chelonia is that between Cryptodira and Pleurodira, based on a difference in the method and degree of retraction of the head. One of the main differences between Polyphaga and other beetles is in the same region, affecting the cervical region and the front of the prothorax, and probably reflects an initial difference in respect of the mode of head retraction—in Adephaga the head is basically strongly prognathous and with little retractability, whereas the original Polyphaga probably had a more inclined head which was reflexible ventrally against the prothorax.

Within the Insecta, interesting analogies of the beetles can be traced particularly in the Dermaptera (and their supposed precursors in the palaeozoic Protelytroptera), the Hemiptera-Heteroptera, and the Diptera. The Dermaptera are the only other insect order with real elytra covering folded wings in repose; the abbreviation of their elytra parallels the condition in Coleoptera-Staphylinidae. The last named family is undoubtedly derivable from ancestors with full-length elytra, in the same way as Dermaptera may be derivable from the extinct Protelytroptera. At least in respect of their defensive functions, the forceps of Dermaptera may be analogous to the pygidial glands of Staphylinidae: in both groups the long flexible abdomen would probably facilitate movement in the interstices of litter, soil crevices, etc., as well as the deployment of its terminal defences.

The hemielytra of Heteroptera to some extent serve the same sort of protective function as beetle elytra; the Heteroptera are the only insect group, other than Coleoptera, in which the winged adults often live habitually under loose bark of trees or are fully aquatic. Like the Adephaga, the Heteroptera probably originated as a predaceous line from previously herbivorous ancestors; defensive glands are fundamental features in both groups, and in both fossil evidence indicates that a common ancestor of all the existing forms will have lived in the Triassic period. In Heteroptera, as in Adephaga, it seems that one of the most fundamental divisions is that separating the aquatic forms (Cryptocerata, cf. Hydradephaga) from the terrestrial ones (Gymnocerata, cf. Geadephaga); both Cryptocerata and Hydradephaga are represented by good fossils in Jurassic rocks. A further analogy concerns the development of secondarily herbivorous habits in both groups. In the Heteroptera, this is manifest particularly in the "trochalopod" series of superfamilies, among which the Lygaeidae seem to occupy a central and fundamental position. Lygaeid bugs are noted as seed-eaters, and in the Geadephaga seed-eating seems to be a general tendency in those groups of Carabidae (e.g. Amarini and Harpalini) which have moved towards herbivorous habits. In the Cryptocerata, one family, Corixidae, seems to have moved away from the typical predaceous habits towards eating detrital materials etc., and a similar phenomenon is manifest in the Hydradephagan families Haliplidae (B6) and Noteridae (B9).

Analogies between beetles and Diptera have a certain element of Hegelian dialectic, if not of paradox. Both groups are outstanding in the diversity of the foods and habitats to which they are adapted, and both are particularly notable for the exploitation of such sporadic and unreliable food sources as carrion, dung and fungi. One might see in the comparison of them the rivalry of two, somewhat mutually exclusive, virtues of patience and energy. Whereas a long-lived beetle may be content to "stay put" in a limited area and patiently await the arrival in it of the right type of food, a typical fly will spend its short life in frantic search with the chance of locating food by covering a sufficiently large area.

Less paradoxical are the analogies of Coleoptera to Diptera in larval adaptations. One field in which these are manifest is the respiratory adaptations of aquatic forms, as has been pointed out by Hinton (1955). The metapneustic arrangement, with a single pair of large posterior abdominal spiracles, opening into a pair of large longitudinal tracheal trunks, seen in so many fly larvae, is also characteristic, e.g. of Dytiscidae (B10) and Helodidae (G3). In the Dryopoidea, almost all the types of larval respiratory adaptations known in the Diptera may be paralleled and, as in Diptera, the lack of a closing apparatus to the spiracles is a general and presumably ancestral feature.

As is well known, the order Coleoptera includes some of the largest living

species of the Insecta (Fig. 3), but it also includes, particularly in the family Ptiliidae, some of the smallest known members of the class. The size range is from a length of little more than 0.25 mm in certain Ptiliidae-Nanosellinae (e.g. *Nephanes titan*) living in the pores of Polyporaceae, up to something like 100 mm in certain Cereambycidae, which parallels the range in the Mammalia, from about 6 or 7 cm in the smallest Rodentia and Insectivora up to 2500 cm or more in the largest whales. Taking the order Coleoptera as a whole, it is probable that the mean or modal body length will prove to be



FIG. 3. *Megasoma elephas* (I10), about half size. (After Berlese, 1909).

somewhere in the 4 or 5 mm range, i.e. at about the geometric mean between the extremes. Of course, some of the divisions within the Coleoptera will have average lengths well above the mean for the order, e.g. the Scarabaeoidea, Cerambycidae, Buprestidae etc., and others, e.g. the Clavicornia, the Myxophaga, various families of Staphylinoidea, etc. would have average lengths per species well below that for the order as a whole. To some extent, size ranges may be used to characterise beetle taxa.

The large sizes, striking forms, and metallic colours, of some of the species are doubtless factors which attracted the attention of collectors to the group in the first place; when it is added that beetles are usually easy to collect, can be collected all the year round in most climates, are relatively easy to preserve in collections, and are on the whole not very difficult for an amateur to identify fairly reliably (at least in most of Europe), it is not surprising that the group ranks second only to Lepidoptera in popularity with amateur collectors, and

has held this position for at least the last 200 years. Mainly due to the efforts of these collectors, the beetle species of Europe, and to a lesser degree of North America, have become one of the best-documented of insect groups, both in respect to the naming of the species and to their detailed geographical distribution. Furthermore, there is a great deal of accumulated information on the habitats and habits of many of the species (e.g. in Horion, 1941–74).

For most of the countries of central and western Europe, key works exist in their own languages whereby all or most of their Coleoptera may be identified to the species level, even though in many cases such works are at present available only in libraries and the second-hand book market. There are few if any countries outside Europe whose total beetle faunas are covered to anything like this extent in published works, but useful key works exist for particular families in many countries, notably the USA, Canada, Japan and India. In the absence of key works, routine identification of species is a much more arduous task, requiring either comparison with already identified collections or tracing of scattered descriptions etc. through catalogues (e.g. the all-important though in many groups sadly out of date “*Coleopterorum Catalogus*” of Junk). The great museum collections of the world, notably those of London and Paris, provide the best possible resources for the determination of beetles from the less well known faunas of the world. Such institutions are commonly willing to provide determinations for beetle specimens from these less-known faunas, on the condition that they may retain individual specimens which might fill in significant gaps in their collections. The best policy for the collector wishing to make use of these museums is first to accumulate a small series of specimens of each species to be identified, then to select a single representative specimen of each (preferably a male), adequately labelled and species-numbered, to be sent to the museum, and to notify the museum of this.

The exceptional diversity of foods and habitats within the order means that a collector, wishing to build up from his own collecting a reasonably complete collection of his local beetles, will be obliged to explore a greater diversity of ecological habitats than almost any other kind of amateur naturalist collector. It may not be altogether accidental that Charles Darwin began his lifelong commitment to natural history as a beetle collector at Cambridge; serious beetle collecting could hardly be bettered as a way of initiating the beginner into the most diverse aspects of natural history and ecology. He will need to fish in all kinds of fresh and brackish waters, explore the inter-tidal zone of the shore, study the nests of owls, woodpeckers, moles, badgers, ants, etc., investigate all kinds of carrion and dung, pay attention to algae and fungi, spiders, Homoptera and Aculeata (for Stylopoidea), all kinds of dead and living trees, forest leaf-litter, caverns, most kinds of Phanerogams, the deeper crevices of soils, human food stores etc. Many species of beetles are markedly seasonal in

their adult activity, and by no means all of these are restricted to the warmer seasons of the year—almost every month of the year is liable to produce its own beetle specialities.

Various ecological relations of beetles are considered in Chapters 13–19 of this book, but more general ecological topics such as population dynamics, energy flow and community structure are not specifically treated here. These and many other topics have been well reviewed—with frequent reference to Coleoptera—in the important recent work of Price (1975) on “*Insect Ecology*”. The classification of the ecological communities of land animals, of which beetles are usually components, was extensively considered by Balogh (1958), who also gives good accounts of the simpler techniques involved in the study of insects in natural communities.

The preparation of beetles for collections is a matter on which there are considerable differences of opinion and practice. The simplest method, pinning, has much to recommend it for the larger species, and is convenient for most beetles, other than Staphylinidae, which are more than about 5 mm long. If pinned specimens are to look well in the collection, it is necessary to use something like a lepidopterist’s setting board to spread the antennae and legs symmetrically. The major disadvantages of pinning are that it offers no protection for the specimen, and that it is impracticable or at least inconvenient for the smaller species. On grounds of both appearance and protection of the specimen, there are great advantages in the sticking of specimens on small pieces of card, by means of gum tragacanth or some other water-soluble glue; properly relaxed specimens can have their legs and antennae symmetrically displayed without the need for a period on a “setting board”. The serious disadvantages of the method are that it precludes immediate observation of very important characters of the underside of the specimens, and that it is rather tiresome and time-consuming when large numbers of specimens have to be dealt with.

The quickest and most convenient method is to glue the specimens to the points of small triangles of card, in such a way that the whole dorsal surface and as much as possible of the undersurface can be seen. No regular “setting” of the appendages is needed, but they should be pulled out sufficiently for all their parts to be seen and so that they do not prevent observation of characters of the ventral side of the body. Specimens mounted on points, though not as exposed to damage as pinned ones, are considerably more at risk than carded ones; they are also much less convenient when large numbers of specimens have to be closely compared in critical species and subspecies work.

The labelling of specimens is also a subject of disagreement. If really full habitat, locality, date and collector details are put on the labels of each specimen, the labels become large and unsightly, and seriously limit the number of specimens that can be put in a drawer or store box. An alternative

method is to put on the label of the specimen merely a number, referring to an entry in a catalogue, in which the full data are entered. This makes for very small labels and a good looking collection, and is quite satisfactory as long as the collection remains in the hands of its original maker. As soon as the collection passes into other hands, however, the danger arises that it will become separated from the relevant catalogue; in any case, it will probably be desired to transfer all or some of the specimens to other collections. Specimens having mere numbers by way of labels are in the long run far less useful than those with the essential data written on the labels.

There is a still small but growing band of collectors of beetle larvae scattered over the world today. Some of them use techniques for the dry preservation of larvae, which can then be placed in cabinets or store boxes with the corresponding adults. These techniques, either by freeze-drying or by dehydration and immersion in xylene, followed by drying, unfortunately produce specimens which are not really suited to critical systematic study. On the whole, the most practicable way of dealing with beetle larvae is to store them, after some type of "fixation" process, in alcohol, with some admixture of glycerine as an insurance against drying out. For critical systematic study, it is almost always necessary to make cleared permanent mounts of larvae (or at least of critical parts of them); these are readily prepared from alcohol material but less so from dry specimens.

Various fixatives (Table 1) have been used for beetle larvae, the most widely used being probably Pampel's fluid (and its variants), Peterson's KAAD mixture, and boiling water. Pampel's fluid has the disadvantage of rather slow penetration, with a consequent tendency of larvae to shrink and contract;

TABLE 1
Fixatives for use with Coleoptera

Petterson's KAAD	– 95% alcohol (or isopropyl alcohol)	– 10 parts
	glacial acetic acid	– 2 parts
	medicinal kerosene (paraffin)	– 1 part
	dioxan	– 1 part
Kahle's Fluid	– 95% alcohol	– 15 parts
	40% formaldehyde	– 6 parts
	glacial acetic acid	– 2 parts
	distilled water	– 30 parts
Weaver & Thomas fixative for internal anatomy	– 40% formaldehyde	– 5 ml
	glacial acetic acid	– 2.5 ml
	chloral hydrate	– 20 g
	distilled water—to make up to	100 ml

Peterson's KAAD ensures rapid removal of the waxy epicuticle and penetration of the body, with a tendency to cause distention and sometimes even rupture of the cuticle. Both fixatives work less well with large fleshy larvae of Scarabaeidae, Cerambycidae, etc., which tend to become discoloured in them; such larvae preserve their appearance much better if they are killed by dropping them for a short time in boiling water.

In making slide preparations of beetle larvae, it is necessary first to dissolve the body tissues, which is done with potassium hydroxide solution (10 per cent is usually sufficiently strong). If the alkali is used hot, the solution of the tissues is a fairly rapid process, but there is danger of serious distortion or damage to the cuticle; for small and delicate larvae, it is better to leave them to soak for 24 hours or more in cold alkali, before a final short heating. After washing out the alkali with distilled water, the dehydration process can be fairly rapid, using only three grades of alcohol, 30 per cent, 80 per cent and 100 per cent. Before the absolute alcohol stage, the head capsule should be detached from the body, ensuring that the relatively viscous clearing agent (clove oil) will be able to penetrate freely without causing the cuticle to crumple. In the clove oil, either the mandibles or the "ventral mouthparts" (maxillae + labium) or both may be dissected off the head. It may be advisable to detach a lateral part of one of the abdominal segments which can be flattened out and mounted separately to give a face view of a spiracle. It is advisable to mount the head capsule separately, under a small supported coverglass, and the trunk similarly under a larger supported coverglass; the mouthparts and spiracle can be mounted separately, under an unsupported coverglass. One systematically important character which can be seen on the unprepared larva but is not properly visible in a normally mounted head capsule is the number and disposition of the ocelli; a small diagram of these in relation to the antennal socket should be made before the potash treatment, and placed on the label of the final slide.

Many beetle larvae are very little if at all pigmented, and their skins are liable to become almost invisible in a preparation such as we have described. In such cases, some type of staining is needed. Perhaps the most useful stain for this purpose is carbol fuchsin, which is usually made up in water and can be used immediately after washing out remains of alkali with distilled water. Larvae should be left in it for at least an hour, and transferred from it direct to 30 per cent alcohol and rapid dehydration—the stain washes out freely in the weaker alcohols, and if staining has been unduly heavy, it can be "differentiated" by leaving the specimen longer in the lower alcohols.

A useful beetle larva collection will probably comprise a large number of specimens in alcohol, plus a smaller number mounted on slides. The most convenient way of keeping the alcohol specimens is to place each specimen (or batch of specimens with the same data) in a convenient sized glass tube,

together with as full a label as possible, to fill the tube with alcohol (with say 10 per cent glycerine admixture) and plug its opening with a tight wad of cotton wool; such tubes may be stored, cotton wool end downwards, in a fruit preserving jar with a layer of cotton wool over the bottom and a filling of the alcohol glycerine mix. The only attention needed for a collection of this kind is an annual check of the bottles, with topping up of the alcohol and, where necessary, replacement of the seal-discs in the lids. Larval slide preparations of the kind described should be stored flat, not in the type of slide box or cabinet where the slides fit into slots edgeways on.

The making of cleared slide mounts may also be very useful in the anatomical and systematic study of adult beetles. It is most commonly practised in the study of male external genitalia (aedeagus), providing a valuable criterion in distinguishing "difficult" species, but may also be used in the study of cuticular structures, including internal ones like endosternites, tentoria, proventriculus, tracheal system etc. In this process, dark-coloured parts of the cuticle can be rendered transparent by treatment with hydrogen peroxide (20 volumes solution). In general preparations of adult beetles, it is advisable to detach elytra and wings at the base, to mount one wing in a folded and the other in expanded condition, to extrude the terminal abdominal structures, to detach the mouthparts from the head, and to detach one leg of each pair (including its coxa). In the process of preparation, remains of gut-contents may be removed and mounted separately, as may the proventriculus if present.

Various other fixation and preservation techniques are employed for special purposes. In dissection for the study of general internal anatomy, it is normally best to use freshly killed (e.g. with ether) specimens, but when this is not practicable, Weaver and Thomas (1956) recommend the use of specimens fixed (preferably after piercing the cuticle at some convenient point) in a chloral hydrate-formaldehyde-acetic acid mixture (see Table 1). For the study of gonial chromosomes (see Chapter 12), the freshly dissected gonads should be fixed for some minutes in a mixture of $\frac{1}{4}$ glacial acetic acid and $\frac{3}{4}$ absolute alcohol, as a prelude to either embedding and sectioning, or the making of squash or smear preparations, in either case to be followed by Feulgen staining.

An essential requirement for the biological study of beetles is the ability to rear the species under controlled conditions in captivity—and for the great majority of existing species, this requirement has still to be met. If a species is to be carried through more than one generation in captivity, the appropriate conditions have to be provided for adult feeding, mating, oviposition, egg development to hatching, larval feeding and ecdysis, pupation, and adult emergence. The requirements for each of these stages in any particular species cannot be determined *a priori*, but only by observation and experiment. Most

“wild” species are much more demanding in these respects than are the stored product species favoured by laboratory experimentalists.

A notable pioneer in the controlled rearing of beetles was the French entomologist and amateur, Eduard Perris, who produced (1877) the first comprehensive work on beetle larvae, and who recorded numerous interesting observations on the development stages of species of most of the main families of the order. His general method was the simple and natural one of trying to reproduce as closely as possible indoors the conditions in which he found the species developing in the field—carried on after his death, e.g. by J. H. Fabre.

Modern laboratory workers have devised various types of foods, including “meridic diets” of precisely known composition, and rearing media often very unlike the natural ones, whereby particular, usually economically important, species, e.g. of Coccinellidae (T25), Cerambycidae (U2) or Scolytinae (V10) can be reared in the laboratory. It has been found that many of the smaller species feeding on mould-type fungi, e.g. in Ptiliidae (F1), Cryptophagidae (T13), Corylophidae (T22) and Lathridiidae (T28) can easily be reared in Petri dishes, given a flooring of damp plaster or blotting paper and a provision of mouldy bread; yeast cultures have also been found to provide good rearing media, e.g. for species of Liodidae (G3).

For herbivores, the prime requirement is liable to be the pot cultivation of suitable food plants; the greatest difficulties are liable to be encountered with subterranean root-feeders, such as pleurostict Scarabaeidae (I10). Eumolpinae (U5), Adelognatha (V10) etc. Carnivorous beetles and larvae, where they will not feed on small scraps of meat, can usually be fed on suitable sized fly maggots; the prevalence of cannibalism in such species makes it advisable as a rule to rear specimens individually in separate containers. The rearing of water beetles in aquaria is liable to require the provision for stages (particularly for pupation) coming out of the water, and also for the females to deposit their eggs in stems of suitable water plants. In a few cases, myrmecophilous beetles have been successfully reared in artificial observations ants’ nests.

Chapter 2

Some Skeletal Peculiarities of the Adults

Every living form is a miraculous mechanism, however, and every sanguinary, vicious or twisted need produces in Nature's workshop a series of mechanical arrangements extremely suggestive and interesting for the engineer, and almost invariably beautiful or interesting for the artist.

Wyndham Lewis, "The Caliph's Design"

As we have seen, the beetles present, in the overall organisation of their exoskeleton, some analogies to the reptilian Chelonia, and incidentally to the mammalian armadillos, and are markedly different from other groups of Insecta. Features distinctive of the order are to be found in the exoskeleton of each of the three main tagmata of the body.

The most distinctive feature of the coleopteran head is its broad ventral closure behind the mouthparts, with the usual presence of a pair of gular sutures extending forwards from the occipital foramen and bounding the gular region. (Fig. 4) Internally, the gular sutures are represented by a pair of flanges, from which the tentorium arises. The tentorium itself is of fairly normal structure as a rule, with a transverse bar (corpotentorium) connecting its ventral parts, the antero-dorsally projecting processes in front of which are often widened to form the "laminatentorium" of Stickney (1921), before giving rise to a pair of dorsal arms leading to the posterior tentorial pits (on the frons) and a pair of anterior arms leading to the anterior tentorial pits, immediately adjacent to the antennal sockets. The gular sutures may at times be reduced to a pair of posterior pits (as in many of the higher Chrysomelidae (U5)), or be partially fused in the mid-line as in many Carabidae (B4), Staphylinidae (F7), Histeridae (E3), Curculionoidea, etc. In some beetles the tentorium is largely membranous, e.g. in Lycidae (O4), Phalacridae (T4), and most Chrysomeloidea, and in a number of groups the corpotentorium is lost. e.g. in Cantharoidea.

Another feature of the head (Fig. 5) which separates most beetles from most other Endopterygota is the position of the antennal insertions. These are commonly, and no doubt primitively, low down and lateral, between the compound eyes and the bases of the mandibles, instead of being more or less

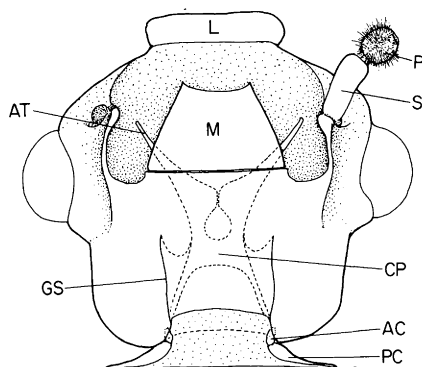


FIG. 4. *Peltastica tuberculata* (P1), ventral view of head, mouthparts removed. AC, anterior cervical sclerite; AT, anterior tentorial arm; CP, corpotentorium; GS, gular suture; L, Labrum; M, mentum; P, pedicel; PC, posterior cervical sclerite; S, scape.

frontal. This is one of the features pointing to originally subcortical or "substrate grade" (Hlavac, 1972) habits of beetles. A third feature is that dorsal ocelli are rarely present, and never three in number, when present, there are usually two (Fig. 5), widely separated from each other and often close to the compound eyes, though most Dermestidae (P3) and the staphylinid *Metopsia* (F7) have a single median ocellus.

The head capsule in some groups carries more or less deep pocket-like impressions in particular positions, for the most part of unknown functions.

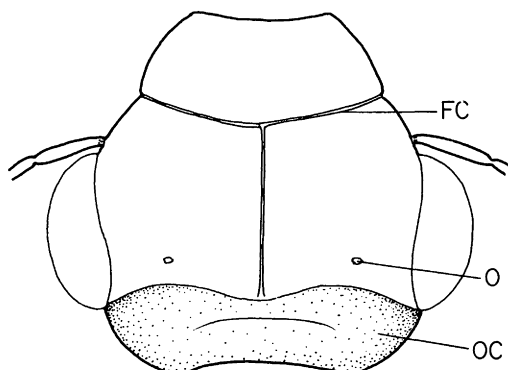


FIG. 5. *Helodraena* sp. (D1), dorsal view of head, mouthparts removed. FC, fronto-clypeal suture; O, ocellus; OC, occipital region normally retracted into prothorax.

Paired pockets more or less closely associated with the antennal insertions are present for example in *Brachyleptus* among the Cateretinae (T1) and *Ctesibius* in the Artematopidae (M1), and a median one on the frons in the Lymexylid *Hylecoetus* (S1); median pockets in the gular region (Fig. 6A) are general in Ptininae (Q2) and Pythidae (T42), and occur also in *Sarothrias* (*Jacobsonium*) (P5)—somewhat similar cavities may also occur in the mentum in some Pharaxonothini (T19). Other Pharaxonothini may show paired ventral cavities outside the gular sutures. Among the Scolytinae (V10) apparently comparable structures in certain species, e.g. of *Dendroctonus*, have been found to function as “mycangia” (see Chapter 17) for the transport of spores or conidia of fungi.

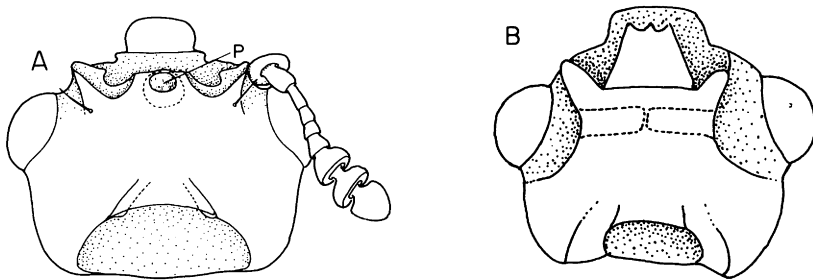


FIG. 6.A. *Floricateres pusillus* (R3), head, ventral view, mouthparts removed, showing pocket (P) in pregular region.

B. *Biphyllus lunatus* (T16), head, ventral view, pregular pockets shown by broken lines.

A rather exceptional type of head cavity is characteristic of the Biphyllidae (T16). These are a pair of long tubular invaginations, extending towards the mid-line from the inner sides of the subocular antennal grooves, and nearly meeting one another in the mid-line, in the anterior gular region, close behind the mentum (Fig. 6B). At least some Biphyllids are fungus-eaters, so it is possible that the cavities serve as mycangia, though I have not seen apparent spores in them.

The structure of the head in adult Coleoptera has been reviewed recently by Bitsch (1973), who, like many other morphologists, relies mainly on muscle insertions as morphological indicators; this criterion, of course, depends on the prior establishment of homologies between the muscles themselves. Bitsch's conclusions to a large extent agreed with earlier ones of Stickney (1923); the later author concluded that true epicranial sutures, corresponding to the ecdysial lines of larvae (see Chapter 5), did not occur in adult beetles, the Y-shaped lines on the top of the head in Hydrophiloidea etc. being of secondary origin.

In almost all beetles (except perhaps for stylopids (S2) the posterior part of the head capsule is more or less retracted into the prothorax, and the retracted

or retractable part is not rarely marked off by a constriction, line or keel from the rest; Stickney (1923) and others have applied the term "occipital suture" to such lines in my opinion are secondary developments with no general morphological significance. The retracted occipital region quite often has a mid-dorsal line, sometimes called a coronal suture; this feature seems often to be associated with a secondary elongation of this part of the head, e.g. in Bostrychoidea and in many types with hypognathous heads.

The occipital foramen in most beetles is relatively large, though in some groups, notably the Aderidae (T45), Anthicidae (T44), Meloidae (T46) and Rhipiphoridae (T38) it becomes quite a small opening, comparable to those of higher Diptera and Hymenoptera. The characteristic and no doubt primitive form of the head in beetles is strongly prognathous, but more or less orthognathous (hypognathous) heads are developed in a number of groups of Polyphaga, notably the heteromeran families just mentioned, the Buprestidae (L1), the Bostrychoidea (Q1), the Chrysomelidae-Hispinae and Cassidinae (U5), the Cerambycidae-Lamiinae (U2) etc., and at least in some of the Hispinae the condition becomes almost opisthognathous, much as in Thysanoptera. The cervical region in the suborder Polyphaga usually has two pairs of cervical sclerites (Fig. 4), lacking in the other three suborders; the differences in this region are probably related to an original adaptation in Polyphaga for reflexing the head ventrally against the thorax, which was not present in the other suborders.

Two important studies of specialised types of head structure in adult Coleoptera are those of Donges (1954) on *Cionus* (V10) and of Kinzelbach (1966) on Stylopidae males (S2), both giving extensive detail on the soft parts as well as the exoskeleton. Kinzelbach in my opinion misinterprets the ventral side of the Stylopidae head, but Donge's interpretation of the *Cionus* head, is in essential agreement with views adopted here.

The somewhat exceptional head-structure (Fig. 7) of male Stylopidae (S2) has been one of the reasons for the exclusion of the group Coleoptera, e.g. by Kinzelbach (1971). Almost alone in Coleoptera, these insects lack any retrac-

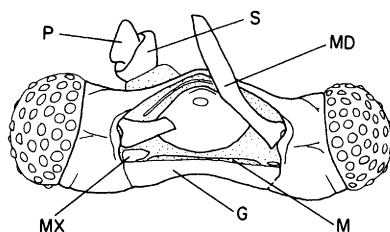


FIG. 7. *Xenos* sp. (S2), male head, ventral view, G, gula; M, mentum; MD, mandible; MX, maxilla; P, pedicel; S, scape. (Redrawn and reinterpreted from Kinzelbach, 1971.)

tion of posterior parts of the head capsule into the prothorax, which itself is much reduced in size as compared with normal Coleoptera. In other Coleoptera, however, the extent to which the head capsule is retracted varies widely (as does the corresponding development of anterior rim-folds to the prosternum and protergum according to Hlavac (1971) and I see no *a priori* reason why it should not in an extreme case be reduced to nil. Kinzelbach further increases the anomaly of the male Stylopidae head by rather arbitrarily interpreting as mentum what I believe to be the gula. He also attempts to interpret various apparent sutures on the dorsal side of the head in terms of orthopteroid head structures—again rather arbitrarily in my view.

The prolongation of the head, before the eyes, to form a rostrum (Fig. 8) is widespread and probably basic in the Curculionoidea (V), and recurs in

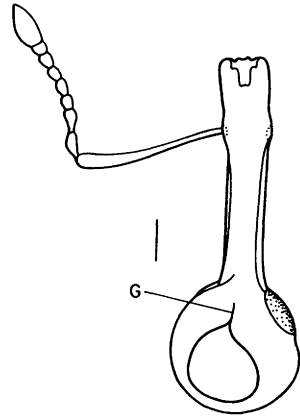


FIG. 8. *Grypidus equiseti* (V10), head, ventral view, mouthparts removed, G, fused gular sutures.

scattered groups elsewhere in the order, e.g. in *Mycterus* (T52), various Salpingidae (T50) and the Laemophloeine *Rhinomalus* (T8) in Cucujoidea, in *Diaphanops* (U4), in some Lycidae (O4), and in the Staphylinid *Tanyrhinus* (F7). In all these cases, the mouthparts are more or less normal and inserted at the apex of the rostrum, and in all except the higher Curculionoidea the antennal insertions are at the base of the rostrum. Some of the rostrate forms, such as *Mycterus*, *Diaphanops* and the Lycidae are more or less floricolous, so that the rostrum may aid them to reach more deep-seated nectaries or stamens, but others, like the Salpingidae, *Rhinomalus* or *Tanyrhinus* are not known to visit flowers. In Curculionoidea, the rostrum is liable to be used in feeding on the deeper tissues of plants, and by the females in making holes in which to deposit the eggs—the rostrum in this group often exhibits sex dimorphism, being longer in the females. The most extreme instance of this is probably in *Antliarrhinus* (V8) (Fig. 9), followed by Brenthididae (V9) and Aglycyderidae (V5).

Grooves adjacent to the lower margins of the eyes, and serving to receive the basal parts of the retracted antennae (Fig. 4), occur in a number of families of Polyphaga and some Carabidae (B4). The genal region of the head-capsule, immediately below the ventral articulations of the mandibles, projects forwards as a more or less prominent tooth in a number of families, particularly among the Cucujoidea-Clavicornia.

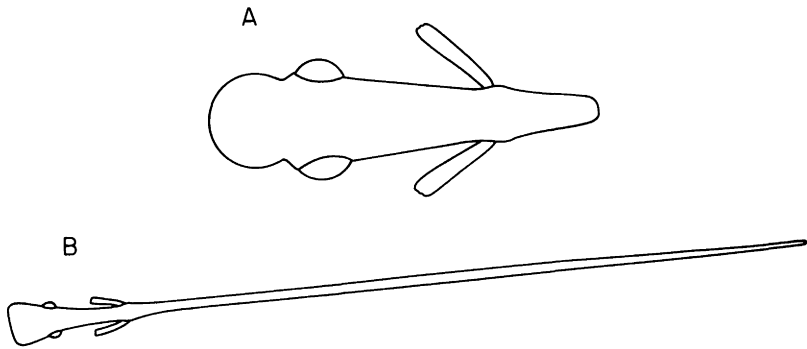


FIG. 9. *Antliarrhinus zamiae* (V8), head, dorsal view. Male (A), female (B), (not to scale.)

Compound eyes are present in the large majority of beetles, but vary considerably in their form. As a rule they are lateral and not exceptionally large, leaving a wide space between them dorsally and not encroaching far on the ventral surface of the head. An anterior emargination, producing more or less kidney-shaped eyes, is common, and may extend so far as to almost or quite divide the eye into two on each side, e.g. in Gyrinidae (B11, *Amphiops* (D5), Clambidae-Clambinae (G1), Acanthoceridae (I3), the cerambycid *Tetraopes* (U2) etc. In some cases, e.g. in many Cerambycidae, such emargination or division of the eyes seems to result from a kind of adaptive "collision" of the eyes with the antennae—selective forces having possibly placed a strong premium on the same position for both organs.

In many beetles there is a transverse groove (Fig. 5) on the upper surface of the head between the dorsal articulations of the mandibles, which has generally been taken as the fronto-clypeal suture. This groove marks the line of internal flange, and its presence is usually correlated with a well developed molar part to the mandibles (*vide infra*) and strong mandibular adductor muscles. There is sometimes a distinct membranous or lightly sclerotised strip between the clypeus and the labrum, which has been called an "anteclypeus" or "preclypeus" (Stickney, 1921) by some authors.

The labrum is a visible and articulated sclerite in most beetles, with the major exception of most Curculionoidea; in particular groups it may become more or less occluded under the front margin of the clypeus, as in many

Scarabaeidae (I10), or indistinguishably fused to the clypeus, as in Eucnemidae (N4), Cantharidae (O10), Curculionidae (V10) etc. In a few cases, the labrum is specially modified in connection with the development of piercing and sucking mouthparts, e.g. in *Aculagnathus* (Fig. 10) and *Cautomus* (T21), the staphylinoid *Myrmicholeva*, the eucinetid *Euscaphurus* (G2), or the myxophagan *Sphaerius* (C4) (*vide infra*).

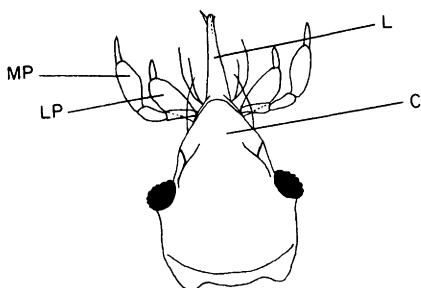


FIG. 10. *Cautomus elongatus* (T21), head, dorsal view. C, clypeus, L, labrum; LP, labial palp; MP, maxillary palp. (Redrawn from Besuchet, 1972.)

Modern beetles are unusual among the major insect orders in having a definite basic number of antennal segments, subject to frequent reductions but to far less frequent increases within the order (cf. Dollo's Law). The basic number is eleven, comprising a usually large scape and smaller pedicel, both these segments with internal muscles, plus nine non-musculated segments of the flagellum.¹ The pedicel in beetles is usually small, with the contained Johnston's organ (see Chapter 8) poorly developed, but certain families may have a large pedicel, e.g. Gyrinidae (B11), Dryopidae (K7), Dasyceridae (F6a) etc. Specialised sensilla, other than ordinary setae, are usually restricted to the flagellar segments, and are often concentrated on a few enlarged terminal ones composing a club (see Chapter 8). Another type of modification of the flagellum is the unilateral or bilateral expansion of most or all of its segments, producing serrate, pectinate, flabellate or biflabellate antennae (Fig. 11); in such cases the sensilla are usually concentrated on the expansions of the flagellar segments. Flabellate antennae seem to be particularly liable to increases in the basic number of segments. The scape in several families may become elongate, with a marked angle between it and the rest of the antenna, giving "geniculate antennae" as in most Curculionidae (V10), Lucanidae (I1) (Fig. 11,d), and many Histeridae (E3).

An antennal length of rather less than half the body length is common and probably modal in Coleoptera. Extremely short antennae, not or scarcely longer than the width of the head, are known in Gyrinidae (B11), various

¹ The lower Permian *Sylvacoleus*, representing a proto-coleopterous stock, had thirteen-segmented antennae according to Ponomarenko (1969) (Fig. 308, p. 659).

Myxophaga, Hydrophiloidea, Dryopidae (K7) and Heteroceridae (K9), some Coccinellidae (T25) etc.; it will be noted that four of the five named groups have more or less aquatic habits. At the other extreme, very long antennae are particularly characteristic of Cerambycidae (U2), where in forms like *Acanthocinus* the antennae may be more than twice as long as the entire body. In many beetle groups, there appears to be a correlation of long antennae with active flying habits.

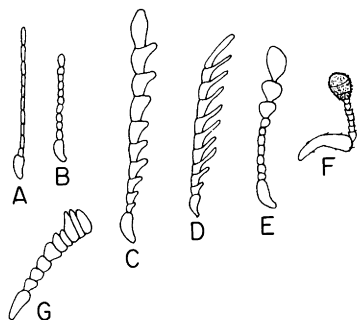


FIG. 11. Antennal types: filiform (A), moniliform (B), serrate (C), pectinate (D), lossely clavate (E), compactly clavate and geniculate (F), with serrate club (G).

A peculiarity which recurs in a number of different families of Coleoptera and which is clearly polyphyletic in origin is the development of an interrupted antennal club, by the enlargement of segments 7, 9, 10 and 11, leaving 8 small. This condition is normal and doubtless ancestral in Liodidae (F3), and is present in a few other Staphylinoid types such as species of *Euthia* (F4) and various small Scaphidiinae (F7); it is possible that in these groups it has been inherited from a common ancestor. A similar condition seen in *Hydnobioides* (T7) and in the Lamprosomatine *Oomorphus* (U5) must, however, represent two further independent developments of it. The adaptive significance of this feature is as yet quite obscure.

The presence of small exocrine glands, each consisting of three cells and with a duct opening on the surface of the cuticle, has been recently demonstrated in the antennal funicle segments of a cavernicolous *Choleva* (F3). These glands are said to be most numerous on segment 7, show no apparent difference between the sexes, and are of entirely unknown function. Some of the histological features noted by Mlle Martin (1975) suggest that the secretion may be proteinaceous. It is noteworthy that antennal segment 7 in *Choleva* would also contain special sensory organs, opening into the sensory vesicles as described by Corbière-Tichané (1974)—these sense organs seem to be rather similar in size and basic structure to the glandular ones, whose openings would presumably lie on the outer surface of the segment.

The mouthparts of most beetles are of a fairly typical biting type, much

resembling those of various Orthopteroid insects. The most marked modifications of the basic pterygotan pattern are the maxillary palpi with four rather than five segments, and the labium never possessing two pairs of apical lobes (glossae and paraglossae); also perhaps the lack of single or paired salivary ducts opening on the hypopharynx.

The basic type of beetle mandible has the usual dorsal acetabular fossa (receiving a condyle at the corner of the frons) and ventral condyle (received in a fossa in the genal region). The primitive type (Fig. 12) is stout, with a broad

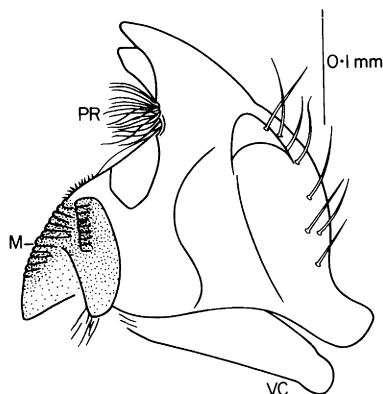


FIG. 12. *Cryptophagus* sp. (T13), R mandible, dorsal view. M, molar part; PR, prostheca; VC, ventral condyle.

base bearing a well-marked sculptured molar area, in front of which lies a frequently, setose area of the cutting edge (corresponding in position and probably in function to the prostheca of the larval mandible), and a sharp apical incisor part with one or more teeth. Mandibles of this type are to be seen in numerous species feeding on moulds, algae, pollen, detritus, etc., but the pattern is liable to modification in species feeding on other animals or on the compact tissues of higher plants and fungi. Most of these latter types have the molar part indistinct or absent. Carnivores are liable to develop more or less falcate mandibles (e.g. in numerous Scydmaenidae (F4), Staphylinidae (F7), and Lampyridae (O8), with widely separated bases (Fig. 13)—the adaptive features of this type of head have been well discussed by Evans (1965).

An exceptional form of the dorsal articulation of the mandibles is general and probably fundamental in the Curculionoidea. Instead of the usual simple acetabular fossa, receiving a simple tubercle of the head capsule, we find a strong tubercle developing inside the acetabulum (Fig. 14), received into a corresponding recess of the head capsule tubercle, thus producing an exceptionally strong articulation. In the Balaninini (Curculionini auctt.) (V10), the articulations are shifted in such a way that the mandibles come to move up and down parallel to each other, like those of Brachyceran fly larvae, rather than biting against each other. The adaptive significance of this feature is not

clear—possibly it might aid the ovipositing female in drilling holes through hard nut shells.

In a number of groups in Cucujoidea, and also in the Staphylinoid Piestinae (F7), the mandibles contain cavities opening to the exterior either dorsally,

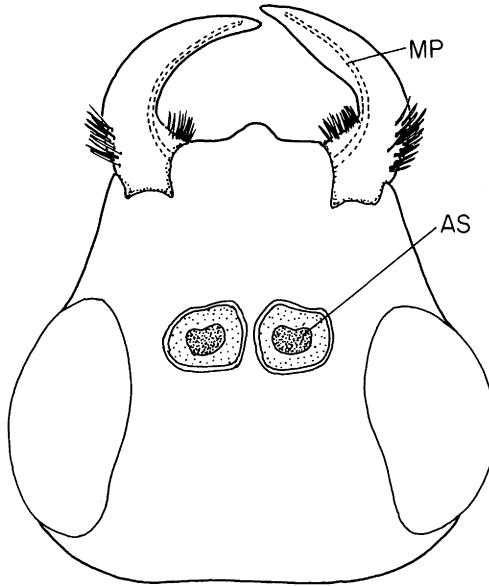


FIG. 13. *Photurocantharis atriceps* (O8), head, antero-dorsal view, antennae and maxillae removed. AS, antennal socket; MP, mandibular channel.

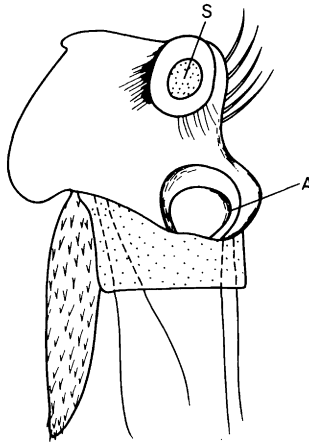


FIG. 14. *Eupagoderes* sp. (V10), R mandible, dorsal view. A, acetabular fossa with central tubercle; S, scar of deciduous mandibular appendage. (After Ting, 1936.)

as in Meligethinae (T1), Sphindidae (T6), Boganiinae (T3), and Uleiotinae (T11) or laterally as in Piestinae and Cavognathidae (T12) (Crowson and Ellis, 1968; Sen Gupta and Crowson, 1969). The dorsal cavities usually have relatively large openings (Fig. 15), are often accompanied by a

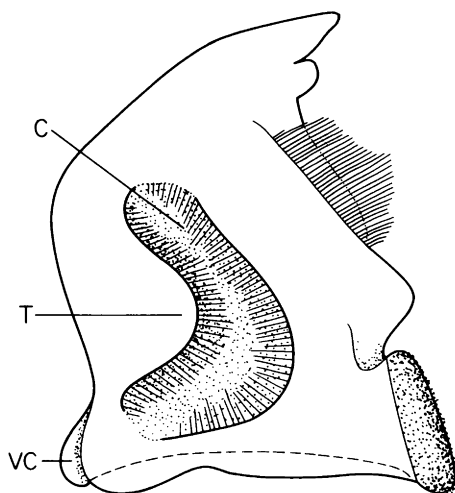


FIG. 15. *Odontosphindus clavicornis* (V10), mandible, dorsal view. C, dorsal cavity; T, dorsal tubercle; VC, condyle.

tubercle fitting into an emargination of the side of the labrum, seeming often, and perhaps usually, to be adapted for the transport of spores (or perhaps pollen grains in *Meligethes*) to new habitats. The laterally opening cavities are generally smaller, and with much narrower openings; they have not yet been noted to contain evident spores.

In adults of most Attelabidae (V7) and in a few other taxa, the mandibles are exodont, i.e. with teeth on their outer edges (Fig. 16). In *Rhynchites auratus* (V7), whose eggs are laid in the stone-fruits of Rosaceae, according to Brack-Egg (1975) the females use the outward teeth of their mandibles in enlarging holes made in the fruit through which the eggs are deposited, but the feature persists in forms like *Deporaus* whose females roll leaves and do not make any hole for oviposition. Exodonty of the mandibles is apt to be less marked in males of Attelabidae, and in *Rhynchites auratus* Brack-Egg (1975) reports that an external cusp on the mandibles is deciduous and lost soon after emergence.

Rather similar deciduous cusps on the mandibles (Fig. 17) are a feature of both sexes of the large majority of Adelognatha (V10), and in this case their function is believed to be in aiding the escape of the adults from the pupal cell, which is normally formed in the soil. These cusps are normally shed fairly soon after adult emergence, but usually leave a characteristic and easily recognisable scar (Fig. 14) on the outer face of the mandibles. Possibly the outer teeth

of the Attelabid mandibles may also serve this function—most if not all species of the group pupate in the soil.

Sexual dimorphism in the mandibles is fairly common in the Coleoptera, and probably in most cases its presence indicates that these organs play an

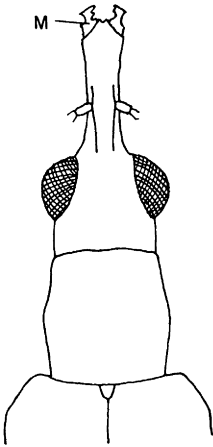


FIG. 16. *Pselaphorhynchites japonicus* (V7), male head, dorsal view. M, exodont mandible. (Redrawn from Morimoto, 1962.)



FIG. 17. Head of teneral *Adelognathan* (V10), dorsal view, showing mandibular appendages (MA) in position.

important part either in courtship or in oviposition. The most striking examples of mandibular dimorphism in relation to courtship are in the Lucanidae (I1), which provide obvious parallels to the antlers of Cervidae, though even in this group there is remarkably little published evidence on the functions of the hypertrophied male mandibles.

Some degree, though often slight, of asymmetry in the mandibles is very widespread in beetles, reflecting the fact that only rarely do the apices of the two mandibles meet symmetrically in the middle line—in the large majority, the tip of one mandible overlies the other. Where the dissymmetry of the two mandibles becomes pronounced, as in some of the Languriinae (T18), the head capsule itself may become markedly asymmetrical (Fig. 18).

A comparative study of the maxillae and labium of species representing most of the families of Coleoptera has been published by Williams (1938),

while Ting in 1936 had studied in rather more detail the mouthparts of Curculionoidea, and there have been many similar studies within particular families. Morphologically, a major problem is that of the homology of the parts of the labium with those of the maxillae. Most recent morphologists have

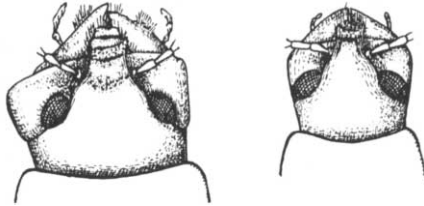


FIG. 18. *Doubledaya viator* (T18), head of male (R) and female (L), dorsal view. (Redrawn from Zia, 1934.)

applied the term mentum to the basal articulated sclerite of the normal beetle labium, but some older authors have homologised it with the maxillary stipites while modern ones usually equate it with the cardines. The distal part of the labium, now generally known as prementum, probably corresponds to the stipites, with palpigers and palps, plus apical lobes.

In the maxillae, the adult cardo is normally an undivided sclerite while the stipes is more or less obliquely divided into a posterior (and outer) basistipes and an anterior (and inner) dististipes; there is usually a distinct sclerite, the palpiger, attached at about the apex of the basistipes, and this bears a typically four-segmented palpus, whose apical segment usually bears a special sense organ on its outer face (see Chapter 8). The galea is typically two-segmented and may attach to the outer apex of the dististipes, to the palpiger, or to both, while the lacinia, when present, is a non-articulated outgrowth of the inner apex of the dististipes, and may bear a strong hooked spine at its apex (Fig. 19).

The mentum (Fig. 20) is normally a large sclerite, broadly articulated to the head capsule, bearing apically the usually much smaller main sclerite of the prementum, to which are directly attached the generally three-segmented palpi (Fig. 20) and an apical more or less membranous ligula, which may be drawn out into paired hairy lobes, especially in floricolous beetles.

(H3), the Psephenidae (K4), many Cantharoidea, the genus *Vesperus* (U1), etc.

Floricolous beetles, e.g. *Cupes* spp. (A3), *Dascillus* (H1), many Ptilodactylidae (K2), some Mordellidae and Rhipiphoridae (T37–38), some Lepurinae (U2) etc., have the maxillary galea (and sometimes the lacinia) and

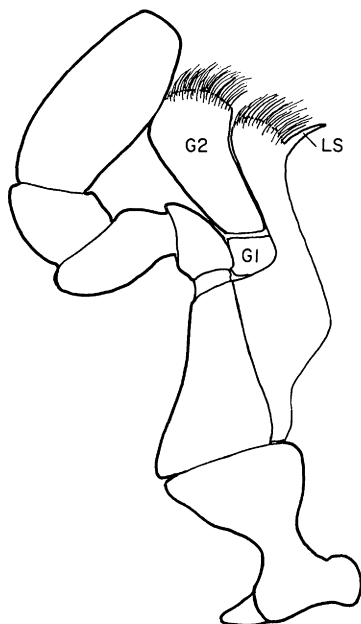


FIG. 19. *Indopeltis nilgiriensis* (R3), R maxilla, ventral view, G1, G2, segments of galea; LS, lacinial spine.

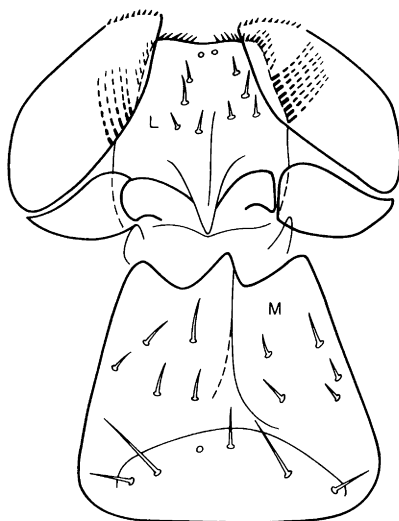


FIG. 20. *Cryptophagus* sp. (T13), labium, ventral view. L, ligula; M, mentum.

often the ligula developed into characteristic elongate hairy lobes (Figs. 21 and 310, p. 662). In some Nemognathinae (T46) the galeae are developed almost as in various bees and Lepidoptera, fitting together to form an elongate suctorial proboscis (Fuchs, 1974; Grinfeld, 1975).

Reduction of the maxillary lobes to one, by loss of either the galea or lacinia, is found in various groups with actively feeding adults. Most frequently lost is the lacinia, as in many Ptiliidae (F1), Lathridiidae (T28), and Cisidae (T33). Loss of the galea is apparent in the Myxophaga, and in most Nitidulidae (T1), excluding the Brachypterinae (Cateretinae). At least in the Nitidulidae, this condition seems to have arisen from a prior specialisation of the galea—in Brachypterinae and in the allied Rhizophagidae (T2), the galea is very narrow and elongate and almost hairless. In the Adephaga, the galea (Fig. 22) is