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CERAMBYCOID LARVAE OF EUROPE AND SOVIET UNION (COLEOPTERA, CERAMBYCOIDEA). PART I.

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Abstract: Available larval material of the superfamily Cerambycoidea (families Cerambycidae, Disteniidae, Oxypeltidae, Anoplodermatidae, and for the present also Vesperidae, although its position is doubtful) of the region has been described and keyed, with notes on bionomics, distribution, and occasionally also classification. For the sake of completeness, the Neotropical families Oxypeltidae and Anoplodermatidae have been included, too. General chapters present detailed morphological characteristics of the families, with some changes in the morphological terminology, and remarks on higher classification of the group.

Part I includes all introductory chapters, families Vesperidae, Anoplodermatidae, Oxypeltidae and Disteniidae, general chapters of the family Cerambycidae, and subfamilies Parandrinae, Prioninae, Necydalinae and Aseminae of the latter family.

Key words: Cerambycidae, Disteniidae, Oxypeltidae, Anoplodermatidae, Vesperidae, morphology, keys, taxonomy, bionomics.

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INTRODUCTION

Main task of the present monograph has been to examine available regional larval material of the family Cerambycidae, to carry out a morphological revision of that material and prepare as reliable larval keys as possible. All our efforts have been determined by and submitted to that aim.

Nevertheless, a number of more general (morphological, taxonomical or other) problems appeared in the course of work, and at least provisional resolving of some of them seemed to be important for more appropriate treatment of the available material. That is why, regardless of the title of the monograph, the general chapters (including introductions to families and occasionally subfamilies) often concern non-Palaearctic groups, too. For the same reason the Neotropical families Anoplodermatidae and Oxypeltidae have been included. Thus I believe that the present monograph might also be useful to entomologists dealing with non-Palaearctic fauna.

Each chapter has been written by only one of us (the authorship is evident from the »Contents«), and the author is fully responsible for its content, although of course we made certain agreements in order to unify the form and extent of the text. Thus, one of us may well disagree with some opinions contained in the chapters written by the other author. I believe this will not disturb the comprehensibility of the text.

The text has been translated into English by the authors. Our thanks are due to Dr. M. Rakovič for making the language revision. However, as some minor changes have been done after this revision, the authors are responsible for all language mistakes.

Illustrations for chapters written by M. L. Danilevsky and P. Švácha have been drawn by G. B. Danilevskaya and the author respectively.

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The present writer would also like to express his personal gratitude to the whole staff of the Department of Systematic Zoology, Faculty of Science, Charles University, Prague, where he almost completed his part of work during his attachment to the Department in 1981 to 85, for making nice friendly atmosphere, so unusual in the present-day world.

The monograph will probably appear in four parts. Part II should contain the subfamilies Apatophyseinae and Cerambycinae (by M. L. Danilevsky), part III - Lepturinae (by P. Švácha), part IV - Lamiinae (by M. L. Danilevsky).

SHORT REVIEW OF LITERATURE

The literature concerning larvae of the family Cerambycidae is relatively rich in comparison with most other families of Coleoptera. This seems to be a by-product of generally greater interest originally apparently caused by the great attractiveness of adults which have been often reared by collectors from larvae.

However, especially some small papers with descriptions of single species often suffered from the authors' lack of deeper insight into the larval morphology which usually resulted in a formal description of a limited value.

Below I am discussing only some authors who have substantially contributed to the subject. Usually by far not all their papers are listed in »References« as many of them have not been directly used for preparing the present paper.

We have chosen the year 1915 as the starting point. From the papers that appeared earlier special mention deserve those of XAMBEU, PERRIS and esp. SCHIÖDTE who succesfully introduced larval characters into the classification of the family. However, in spite of the value of their papers at the time of appearance, particularly with respect to the fact that they called attention to the study of the immature forms, they cannot be used as a serious source of information on larval morphology at the present time.

In 1915, CRAIGHEAD published his paper on the larvae of North American Prioninae, which was followed by two other papers (1916, 1923). These three papers are the most significant point in the study of Cerambycid larvae, and very few subsequent papers have reached their quality. CRAIGHEAD proposed an excellent morphological terminology based on detailed studies (including musculature - 1916, slightly adapted 1923) which has been, with small corrections, used also in the present paper. Unfortunately, some subsequent authors used other, much more primitive morphological terms.

Soon after, probably stimulated by the above CRAIGHEAD'S studies, very good papers on Indian (BEESON, 1919; GARDNER, many papers) and Japanese (T. KOJIMA, 1929, 1931) Cerambycid larvae appeared, which substantially contributed to our knowledge of the morphological variety of larval forms from other regions of the world.

An enormous contribution in a similar direction has been added by the series of monographs by DUFFY (1953 to 1980), which also indicated some more discrepancies in the existing traditional classification, although DUFFY himself was very reserved regarding such problems. His activities also resulted in a very large and valuable world larval collection, now mostly housed by the British Museum.

Among smaller more geographically and/or taxonomically restricted papers I should mention e.g. the larval keys to British species (EMDEN, 1939–40) and French genera (PAULIAN, VILLIERS, 1941), both, however, containing some errors, papers by TEPPNER, most comprehensive of which is the key to European Lamiinae (1969), or some papers by DEMELT (esp. 1966) which, however, are more aimed at

bionomical data and which lack keys or detailed descriptions. I also wish to call attention to the precise and nicely illustrated paper by DUMBLETON (1957) on some New Zealand Cerambycid larvae. A number of short papers have been published for many parts of the world, I remind here e.g. the series of papers by PALM (1951 to 1960) who first discovered habits of some interesting larvae of Lepturinae. Other smaller papers (mostly not included in References) appeared in Europe, USSR, India, Egypt, North America, Brasil etc.

Unusually numerous larval studies have appeared in the last three decades in Japan. Unfortunately, unlike the above mentioned papers of T. KOJIMA, they are almost all in Japanese which makes the data inaccessible to most other workers. Many nice illustrations can be found e.g. in the monograph by K. KOJIMA and HAYASHI (1969).

Paradoxically, the Palaearctic Region had to wait for a more representative monograph till middle of the seventies. The book by MAMAEV and DANILEVSKY (1975), concerning the fauna of the USSR, included many species occurring also in the other areas of Europe, in Japan, North China etc. Regardless of a few errors, this monograph surely belongs to the best ones published on the subject.

After numerous shorter papers (usually jointly with his wife), A. I. CHEREPANOV has recently published the six-part monograph »Longhorned beetles of North Asia« (1979 to 1985) covering the Asian part of the USSR except for Central Asia. In this monumental work concerning also larvae he summed up the immense quantum of data collected by him and his collaborators during many years of field work from Ural mountains to the Soviet Far East. Every reader must be simply stunned by the quantity and completeness of the material. The unique bionomical data are out of competition, and are often used by us in the present paper. Almost every species has been provided with nice illustrations of larva, pupa and the adult drawn by A. Z. Ermolenko.

Unfortunately, such words of praise cannot be used when speaking about morphological part of the book, namely about larvae. The morphological terminology used is occasionally incorrect, descriptions are often inconsistent, lacking important data and repeating unnecessary ones. Worst of all, the larval keys, including those to higher taxa, have very often proved unreliable or pronouncedly incorrect. These faults unnecessarily diminish value of the otherwise extremely interesting book.

MATERIAL AND METHODS

Selection of the region dealt with has been limited by our ability to obtain representative larval material. We had to omit the South of the Palaearctic Region as we do not know any larger available collection, although we have occasionally included species from that region (e.g. Canary Islands, North Africa, Asia Minor) if they were at our disposal. Larvae of many species have been collected in Japan, but obtaining good Japanese material would be difficult and time-consuming for us, in fact I feel the job should be done by the Japanese authors themselves.

The present monograph has been based mainly on the collections of the A. N. Severtsov Institute of Animal Ecology and Evolutionary Morphology of Academy of Sciences of the USSR

in Moscow, and of the present writer (P. Švácha). We are deeply indebted to all who helped to fill numerous gaps by presenting us additional material, often very large and valuable, both from their personal collections and from collections of their institutions. Nevertheless, larvae of many species are still to be discovered.

Some collections from the region remain inaccessible to us. Among them by far largest is that of the Biological Institute of the Siberian Branch of Academy of Sciences of the USSR in Novosibirsk, which served as a base for the monograph by CHEREPANOV (1979 to 85, see review of literature). Unfortunately A. I. CHEREPANOV decidedly refused loan, exchange or any other cooperation. The collection contains a number of species completely absent in our material, and additional specimens of some other species would be much welcome as well. Other unavailable collections are of much more limited value.

Regarding published descriptions of species lacking from our material (which are mainly those described by Cherepanov, l. c.), we sometimes bring the information available from the descriptions and drawings, but we found it usually impossible to include these species in our keys due to a lack of data about certain characters used by us.

We have in our paper greatly reduced all non-morphological data (bionomics, distribution etc.) in order to limit the extent of the text. Published host plants are listed only if the authors undoubtedly observed immature stages or at least reared adults. Earlier authors often deduced the host plant from indirect observations, and such approach led to many errors, frequently repeated by further authors. Even then the list of host plants may be often incomplete, particularly if the species is clearly polyphagous - it was not in our intentions to prepare full lists of known host plants.

There are two possible methods how to obtain larval material. Firstly, rearing larvae ex ovo under laboratory conditions, either on a natural host or using various artificial media. This method has an advantage in that we obtain reliably determined larvae of various instars and that adults can be often found more easily than larvae in the nature. However, it is often difficult to find suitable food for species with unknown habits (which also continue to be unknown), and occasionally there may be a rather large portion of aberrant individuals when rearing them on unsuitable media.

Secondly, searching for the larvae under natural conditions. Main advantage is that we, along with the larvae, also obtain data on the species' habits, i.e. about its function in the nature. Main disadvantages are hard work, greater uncertainity about results, necessary rearing of an adult specimen (inducing transformation of larva into adult is usually the most difficult point in the whole rearing procedure, and even then a beginner with little or no comparative material and knowledge cannot be quite sure about whether his larvae are really conspecific with the reared adult). Larval exuvia collected from specimens which have transformed into adults (and are therefore usually easily determinable) are very useful for verifying larval determination or sorting mixed larval material.

Almost all our material has been obtained by this second method.

Collecting and rearing methods vary considerably according to habits of individual species and anything can hardly be said in general. I do not feel necessary to repeat some basic data about collecting and rearing typical xylophagous species - the reader may consult e.g. DUFFY (1953). I am going to mention only some groups with less typical habits.

Some seemingly xylophagous species, particularly certain Lepturinae, are apparently connected rather with some wood fungi. (E.g. the larva of *Grammoptera abdominalis* seems to be found exclusively in oak branches or thin stems infested with the fungus *Vuilleminia comedens*.) Prolonged breeding of such species is rather difficult, as in changed conditions the fungi usually die out, or are substituted by other ones, as a rule non-beneficial to the larvae. In these cases, it is necessary to breed larvae in as large pieces of food material as possible to prevent quick changes of conditions, and to keep all parameters as close to the natural ones as possible. One Lepturine

species (*Pseudovadonia livida*) which has left the wood and develops in soil with mycelium of the fungus *Marasmius oreades* has been successfully reared by BURAKOWSKI (1979) in glass jars filled to one-third with the fungus-infested soil.

Some soil-dwelling larvae feeding on roots of herbaceous plants have been successfully reared by the author in glass tubes stuffed with root fragments. The larva may be transferred into another tube with fresh roots if necessary. A similar procedure may be used for species living in rotten wood (a tube or other suitable vessel filled with wood particles), but not for those living in sound wood, and it is also not very suitable for subcortical species, or only the cambium tissue must be used filling the tubes. Larvae must be placed in tubes strictly separately. This method is rather toilsome and time-consuming and should be used for breeding of rare valuable larval material (a possibility of individual care for each larva).

Many troubles cause the species which leave their food material and go to pupate in the soil. They must be bred in containers with sufficiently deep bottom layer of selected sifted soil. Soil types with very fine particles (clay etc.) are not recommended since they contaminate the larvae which may cause difficulties with ecdysis. The soil should be also tested for its tendency to become mouldy when kept wet, and mould-resistant types should be used. Light sandy soils seem to be the most suitable ones, however, the proportion of sand must be kept sufficiently low to enable larvae construction of rigid non-breaking pupal cells.

Contrary to the general opinion, rearing of endophytic species feeding in herbaceous plants (*Agapanthia*, *Phytoecia* etc.) has proved not too difficult providing the stems or roots are not collected too early. When harbouring half-grown larvae, the plants or their infested parts are mostly already dying out, and we can safely bring them home. Rearing conditions may be similar to those used for species living in dead branches. Moderate moisture is required, and it is also useful to keep the roots or stems above the bottom of the container to prevent contact with condensed water (this is also true for wood-feeding species, particularly if there is no bottom soil layer or some mould-resistant water-absorbing material).

However, it is occasionally not so easy to find these larvae, namely the types going sooner or later down to roots (*Phytoecia*). The reason is usually simple - the mature larva descends underground and will girdle the stem just above ground level which cause the upper part of the plant to break off. This is a protective device by which the larva prevents the possibility of breaking of the stem (by wind etc.) in the region of the pupal cell. Had the upper part been once broken off, the root with the larva can be found only accidentally. Therefore the best period for collecting the larvae is late summer when the upper parts of the infested plants, although often already lying on the ground, mostly still remain connected with the roots.

Another difficult point in rearing the adults is breaking of the diapause. Most species are diapausing as mature larvae (usually in their pupal cells already), more rarely in pupal or adult stages. Species from temperate regions usually require about 2—3 months of cold treatment (about zero level). Natural winter conditions with fluctuating temperature are much more effective than constant temperature in a refrigerator. When adults hibernate in the nature, they are usually incapable of reproduction without cold treatment.

Numerous attempts have been made to accelerate the often relatively slow development of the larvae, either by rising temperature, enriching the food material or breeding larvae on purely artificial diets. As to the latter method, the reader may consult some papers dealing with results of such experiments (BERRY, 1972, GARDINER, 1970b, HADLINGTON et JOHNSTON, 1974, HATCHETT, JACKSON et BARRY, 1973, PAYNE, LOWMAN et PATE, 1975). The larvae feeding in wood seem to be often limited by available nitrogen, and enriching of the wood with e.g. amino-acids or peptides has been referred to yield good results (BECKER, 1938). However, this cannot be applied in species requiring higher moisture because of the nitrogen-containing substances stimulating fungus growth. Accordingly many Cerambycid larvae will readily accept animal food. Some subcortical larvae may occasionally devour other insects, cannibalism is not infrequent.

Many species require adult food to attain sexual maturity which must be kept in mind when we intend to obtain larvae from eggs. Eggs are usually laid on the food substrate, but females of many species will lay them almost anywhere when they are not allowed to select a suitable site.

A few words need to be said about preservation and storage. Cerambycid larvae with their generally soft unsclerotized body require special treatment. The procedure usual in other insects (although even there not very suitable), i.e. to merely put the larvae in 70–80 % ethanol, is entirely insufficient. Larvae thus preserved mostly lose their natural colour (darken), and become often so contracted that many characters are very difficult to study. Legs, antennae and palps often break off, and dissection is almost impossible, since all parts of the body become hard and fragile.

I mostly use (even during field works) the following procedure: The larvae are killed by immersion for about 2–20 seconds (according to size) into hot water (about 80–90 °C, boiling water just put off from the fire), then perforated once or twice in lateral intersegmental zones to prevent osmotic deformation (the instrument for making the incision must be provided with a very sharp and slender point) and put in the so-called Pampel's Fluid (IMMS, 1939, cited after DUFFY, 1953):

glacial acetic acid	4 parts
distilled water	30 parts
formaldehyde	6 parts
ethyl alcohol (95 per cent)	15 parts

DUFFY (l. c.) has not mentioned the concentration of the formaldehyde, consequently it should be supposed to be of 100 %, I use 40 % aqueous solution in the same proportion (6 parts) with good results.

Some specimens (particularly those shortly after moulting) may collapse when picked out from the hot water - then they must be allowed to grow cold slowly in the water.

It is advantageous to slightly narcotize the larvae before immersion in the hot water, using the same chemicals as for killing the adult beetles (e.g. ethyl acetate), as the larvae will not twist, contract thoracic sternum or retract the mouthparts. However, care should be taken to narcotize the larvae only till they cease to move, not longer - their body turgor should be preserved, otherwise some protuberant body structures may collapse and become folded.

To save time and labour, specimens may be simply immersed in the Pampel's Fluid, but the results are not so good, although much better than when using ethanol alone.

I prefer to keep specimens permanently in the Pampel's Fluid, as spirit may cause some unwanted changes even in the already fixed larvae.

Contrary to ordinary use, I keep my larvae in glass tubes with plastic stoppers, not in tubes plugged with cottonwool and placed in a jar filled with the preserving medium. It is much more pleasant to work with such material as one can avoid continuous contamination of hands with the fluid used; in fact the latter alternative cannot be at all used if one wants to keep the larvae permanently in fluids like the Pampel's destructive to human epitheliums (for this reason the larvae preserved in the Pampel's Fluid must be of course examined in a dish with spirit - the evaporations of the Pampel must not be inhaled or get in the eyes). During prolonged storage, however, even the stoppered tubes should be kept in some air-tight containers.

I never use any type of dry preparation.

As much data as possible should be included right in the tube with larvae. Numbers referring to notes in some field diary should on no account be used, or only for additional detailed data which could not be quoted on the label. Catastrophic results caused by eventual loss of such diary are obvious, not speaking about the difficulties after the collector's death when such notes are lost almost invariably.

Finally some remarks on both making and using the descriptions (some of these remarks, however, concern only the chapters written by me).

I was trying to make the description of the general morphology of the family Cerambycidae, and to some extent the subfamily descriptions as well, fitting not only for the region dealt with in the present paper. On the other hand, generic descriptions are mostly based more or less exclusively on the species actually described by us. Excepting some special cases we have not been trying to obtain available non-Palaerctic larvae of the genera employed in the present paper. Such approach would bring us almost insuperable difficulties. With the present state of the family classification it may well happen that some non-Palaearctic species treated in Palaearctic genera actually belong to other ones, and vice versa. We would have to carry out an extensive revision of world larval material (often hardly available) which is impossible for us at present. Moreover, the extreme scarcity of available larval material from many regions of the world would turn such effort to little value anyway. For the same reason - I mean the scarcity of known larval material - I wish to ask the reader not to take the descriptions as a dogma but as a temporary device to be corrected and completed.

During routine work the larvae have been mostly examined with the aid of a stereoscopic microscope with up to 100 x magnification, and such optics would be often needed also for the determination, although we have mostly used the most obvious characters found providing it was not in contradiction with reliability of the key.

In very small species, and particularly in very young larvae such magnification will often fail to show the needed details. I should remember that in some microscopical surface structures which could not be quoted on the label. Catastrophic results caused by eventual loss of such it is hard to be sure they are really absent. Then we can use a compound microscope, but we are forced either to make slides or to procure special equipment for vertical illumination.

Unfortunately there is another difficulty which cannot be overcome by better optics, namely the growth variability. Young larvae of different species are more similar to each other as compared to mature ones, they may miss to some extent the characteristic look or some characters of the mature larvae. In the descriptions and keys such characters are often provided with »in later instar larvae« or a similar warning; however, almost all characters are subject to growth variability main expressions of which will be found in close of the general morphology of Cerambycidae - they must be always kept in mind during determination. Unfortunately there is no general way how to distinguish young larvae of a large species from mature larvae of a small one.

Distinctness of many body characters of the practically unsclerotized Cerambycid larvae depends very much on how they were preserved. Thus, some dividing lines may be very distinct on contracted larvae but almost invisible in extended ones. The same structure (e.g. the ambulatory ampulla) may look quite differently, beginning from the degree of protuberance and ending with the macroscopic pattern. In contracted larvae some body regions (particularly the pterothoracic dorsum) are so folded that their study is simply impossible without damaging the larva.

Moreover, some body surface structures are poorly visible due to almost complete lack of body pigmentation. Surface of larger larvae may be dried up for a moment, certain fine structures (e.g. microscopic spines or pleural discs) become much better observable. Also some staining methods could be recommended. No suitable stuff has been found for staining the cuticle externally. After testing numerous chemicals, the writer uses ordinary black ink for fountain pens manufactured by KOH-I-NOOR Hardtmuth, Czechoslovakia. The ink may be injected inside the body, or the larva may be cut along one side and immersed for longer or shorter period in more or less concentrated aqueous solution. According to these conditions we obtain pale bluish shade to dark blue-black colour, usually with fine metallic glimmer making the surface sculpture very plastic and distinct. The stuff is advantageous by its ability to spread in a few hours or days on whole body surface regardless where injected, and also by the affinity to membraneous regions. The stained material cannot be cleared by ethanol or other chemicals contained in the Pampel's Fluid, in fact no clearing chemical was found, and the stain is very permanent. FRAGOSO (1980),

describing staining with »Parker ink, permanent black«, writes: »In case of over-staining, a mild solution of »Chlorox« (hypochloride) will gradually clear both stains« (i.e. Parker ink and fuchsin in that case).

First instar larvae usually differ substantially from the subsequent instars; they are neither described nor they can be determined by the present paper. They can be often distinguished owing to special devices for escaping from the egg - the so-called egg-bursters or hatching spines which are usually found on the sides of some thoracic and/or abdominal segments, or on the head (for more details consult e.g. DUFFY, 1953, or GARDINER, 1966).

Some descriptions lack certain data (epipharynx, cranial proportions etc.). In such cases we had at hand unique specimens, mostly on loan, and we did not want to dissect those larvae. In all other descriptions, the characters requiring dissection are described from but a very few specimens, not from all specimens available (except when used as key characters), and even such gross characters as e.g. the cranial proportions have been found rather variable. The reader should also pay attention to the »Material« listed in each species, and always await greater variability than described if we had at hand limited number of specimens.

Larval measurement is another source of inconsistencies. Actual length of a badly preserved larva may differ from its natural length by almost 50 % both plus and minus, and natural length of the soft-bodied Cerambycid larvae is also hard to define (e.g. almost all larvae shorten before pupation). Maximal adult length of a species can be found in most taxonomic works - it will help to make an idea of maximal possible size of mature larvae. We usually give in descriptions maximal length found among available larvae, but there are often no mature larvae at our disposal. Like so many xylophagous insects, most Cerambycidae are extremely variable in size.

Cranial proportions are given as follows: »Cranium transverse (1.6—1.8), moderately depressed (2.0—2.2).....« which means: Width/length ratio about 1.6—1.8, width/height ratio about 2—2.2. In the ventral sclerite (gula + hypostoma) the number in brackets giving the width/medial (gular) length ratio. All the numbers holding predominantly for later instar larvae.

Throughout the text, »±« has been used in the sense »more or less«.

The key couplets marked with »!« deserve special cautiousness.

In the paragraph »Material«, the abbreviations are used as follows: SU - Soviet Union, CS - Czechoslovakia, lgt. - collected by, coll. - collection of (not collector!), D - Danilevsky, S - Švácha, IS - A. N. Severtsov Institute of Animal Evolutionary Morphology and Ecology of Academy of Sciences of the USSR in Moscow. For example: 24. 6. 1981 SU, Ussuri region, Suputinka Nature Reserve, 5/I, *Betula,* lgt. D, coll. IS. »5/I« means five preserved larvae determined through imago (reared or found in pupal cell along with the larvae). The symbol »+« on the left side before fraction line stands for greater number of larvae, »—« on the right side indicates that the larvae have not been reared and have been determined by elimination or comparison with other determined material (then a note is often given about reliability of the determination). In some loaned specimens, however, many data are unknown to us.

Scales for drawings are given in millimeters.

Taxonomic data (such as data on type species of the genera, authors of names of the family category etc.) have been drawn from various papers cited in »References«, and have been believed to be correct unless contrary information became available, i.e. the original literary sources have not been consulted as a rule. Some errors are therefore possible, but there has been much work done in the recent years by various authors to make these data agreeing with the International Code of Zoological Nomenclature. In a few cases the needed data were not available, or were deduced from other indirect information available, then provided with a question mark. Names of authors of individual taxa are not abbreviated except for LINNÉ (L.) and FABRICIUS (F.).

NOTES ON HIGHER CLASSIFICATION

Although this is not a taxonomic paper, a short chapter on higher classification seemed useful for several reasons. Of course we had to use a concrete family and subfamily classification in the present paper; this classification, however, arose as a result of compromise, both between the authors and with the approaches most frequently found in recent taxonomic papers (I do not agree fully e.g. with the present subfamily dividing of the Cerambycidae). Moreover, examination of great diverse larval material necessarily resulted in the need to comment upon some taxonomic problems. Particularly in this chapter I must emphasize once more that below I am presenting my own points of view, and my colleague M. L. Danilevsky must not be automatically supposed to share these my opinions.

1) Family grouping: The following families are recognized in the present paper, all once classified under Cerambycidae: Vesperidae, Anoplodermatidae, Oxypeltidae, Disteniidae and Cerambycidae. The former four families sharply differ from the Cerambycidae by complete absence of the gular bridge (submentum directly connected by membrane with prothoracic praesternum) and by hypertrophied plate--like metatentorial bridge forming large portion of ventral cranial wall. In Cerambycidae the hypostomal plates are always bridged by a longer or shorter sclerotized gula, and the metatentorial bridge is at most moderately broad (cf. the Parandrinae and Prioninae). There are two main problems:

a) Is the absence of gula always primary in the four small families? and

b) Is the gula of all Cerambycidae homologous?

I am convinced that the first question should be answered »yes«, and at present I see no serious reason for suspecting homology of the origin (not of the present extent!) of the Cerambycid gula. (However, since the larval gula has been undoubtedly developed several times in the evolution of the Coleoptera, the possibility of parallel development of the Cerambycid gula should not be completely ignored.) Moreover, each of the four small families has other important characters distinguishing it from all Cerambycidae.

Genealogical relations of the four families to the Cerambycidae, as well as their interrelations, are unclear to me. The family Vesperidae lacks any Cerambycid specializations, differing in principal characters from all other present families, and should be no longer treated in the Cerambycoid complex. On the other hand, the Disteniidae may be rather closely allied to Cerambycidae. The broad metatentorial bridge (interpreted quite correctly by both CRAIGHEAD, 1923, and BÖVING et CRAIGHEAD, 1931) has been by some subsequent authors misinterpreted as a »concealed gula« or »concealed hypostoma« (the term »hypostoma« or »hypostomal bridge« should not be used for the medial ventral sclerotized cranial region, since it seems evident that the two hypostomal halves were bridged by material of non-hypostomal, and apparently even non-cranial origin, see the general morphology of the Cerambycidae). This incorrect interpretation also occurred in the recent treatment of beetle

classification by LAWRENCE et NEWTON, 1982, p. 283: »The isolated position of Disteniidae is indicated by the structure of the larval head, in which the hypostoma is concealed beneath the prothoracic skin, the latter being attached directly to the submentum (BÖVING, CRAIGHEAD, 1931).« Curiously, the authors refer to the paper where the structure is correctly interpreted as the tentorial bridge. In this respect the ventral cranial structure of *Distenia* does not differ principally from the typical Chrysomelidae, or many other beetle larvae lacking the gula, except for the width of the tentorial bridge.

LAWRENCE and NEWTON (l.c.) accepted the family Disteniidae in the sense of CROWSON (1981), i.e. including Oxypeltinae, Vesperinae, and tentatively also Philinae. I do not agree with joining of any of these groups into one family as they differ as much one from another as from the Cerambycidae. CROWSON (l.c.) brought no reason for his grouping, but he might have been also affected by the false concept of a concealed gula. The lack of gula is considered primary by the present author (not a single feature has been found in the cranial morphology of the four small families suggesting the possibility of the gula having been secondarily lost), consequently plesiomorphic, and cannot be used as an evidence for relationship of the above families. They possess one single joint character which could be at all regarded as a synapomorphy, namely the extreme width of the metatentorial bridge. However, the difference in that character between e.g. Cerambycidae and Oxypeltidae seems comparable with that between Oxypeltidae and Anoplodermatidae, and I tend to regard the broad tentorial bridge to be a similar and independent response to general need for greater rigidity of the cranium. After all, very broad tentorial bridge may also be found in other (esp. wood-boring) groups, e.g. in many Bostrychoidea or Curculionoidea. Regarding Philinae, their larvae remain completely unknown which is the greatest gap in our knowledge of the Cerambycoid complex. Despite a great effort I was unable to discover any available larval material, or any person in a position to help me with obtaining these larvae. I would like to use this opportunity and to ask the entomologists working in the region of occurrence of the genera *Philus* and *Mantitheus* (essentially the Oriental Region) to pay a great attention to their immature stages. I would be personally indebted for any material or useful information. The found of larval Philinae may well lead to great taxonomic changes.

2) Higher classification of the Cerambycidae: The main difficulty seems to be our frequent inability to determine which (if any) of the known existing states of a character should be regarded as plesiomorphic. Moreover, we are apparently facing numerous parallelisms which makes the situation still more complicated.

Firstly, I feel a great difference between Prioninae s. l. (incl. *Parandra,* see below) and all other Cerambycidae, particularly in the ventral structure of the head capsule. In Prioninae the metatentorial bridge is always rigid, relatively broad, lying entirely in the ventral plane of the cranium. In all other subfamilies its medial portion is very narrow, often only ligamentous, and even in the Cerambycine type slightly sunken into cranial cavity. Another sharp difference is the type of the main antennal sensillum

on the second segment - the latter sensillum always flat or rarely roundly convex in Prioninae, always distinctly conical in all other subfamilies.

I do not agree with the concept (DANILEVSKY, 1979a, similar opinions expressed by some earlier authors) placing Cerambycinae closer to Prioninae than to other Cerambycidae. All transitional tentorial types can be found between the typical Cerambycine type and the Lepturine type with the tentorial arms fully internal - - some Cerambycinae have the tentorial arms distinctly oblique, such types as *Blosyropus* (Cerambycinae), *Opsimus* (?Cerambycinae, see chapter on problematic larval forms) or even *Anisarthron* (Aseminae) are pronouncedly transitional. On the other hand, not a single transition is known to me between the Prionine and Cerambycine types (larvae of the Philinae which might perhaps fill this gap are unknown - see above). The postnotum of Prioninae and Cerambycinae (incl. Apatophyseinae) must have originated independently (in connection with deep retraction of the head?) as it is absent in some Prioninae incl. *Parandra.* The occurrence of certain Prionine characters (separate epistoma, vestigial postcondylar carina, certain similarities on labiomaxillary complex) in some Cerambycinae (chiefly some Cerambycini), if homologous at all, may involve plesiomorphic characters.

Two main types of strenghtening of the ventral cranial wall have been apparently used, mostly excluding each other, namely the development of a very broad rigid tentorial bridge (all four non-Cerambycid families) and development of the gula (all Cerambycidae, but the Prioninae and Parandrinae are interesting by their cranial structure intermediate between the above two types). (The third type of increasing rigidity of the cranium, namely the broad sclerotized hypopharyngeal bracon, is never found in the Cerambycoidea.) When prognathy has been developing (all present families except for Vesperidae), then in the first »metatentorial« type it has been inevitably connected with deep retraction of the head into prothorax. This type also does not allow to produce strongly depressed subcortical forms which require »internalisation« and reduction of the tentorial bridge to make room for the nerve cord (cf. Fig. 8G). Indeed, true subcortical forms are known exclusively in the »non-Prionine« Cerambycidae, particularly in Lepturinae where the internalisation of the tentorial bridge has reached a comparatively highest degree. This process was connected with moving of the spots of invagination of the metatentorial arms from an almost »postcranial« position (in which they actually still are in Prioninae and nearly all Cerambycinae) towards a cranial position which resulted in forming ± distinct metatentorial pits. (In this point it is not important whether we interpret the process as moving of the metatentorial arms or as sclerotization of postmetatentorial region.) Since the absence of gula must be considered plesiomorphic in comparison with its presence (the theoretical possibility of the secondary absence of the gula has been touched above, and rejected because of lack of any relevant demonstrations), and because a rigid, relatively robust metatentorial bridge can be found in many Coleoptera larvae lacking the gula, I consider the Prionine cranial type as the most primitive among the Cerambycidae (as presently defined), and the

type with ± internal metatentorial arms and distinct metatentorial pits as the derived one. I wish to call attention to the fact that there are, as far as I know, no Coleoptera larvae possessing the combination of the presence of distinct metatentorial pits and absence of the gula, or at least of a distinct tendency to develop such structure, whatever its origin (post-labial, labial, in my opinion not cranial) might be in individual cases. This indicates that distinct »cranial« metatentorial pits originate with (or after) the gula.

Although used in the present paper, I do not agree with separating of the subfamily Parandrinae. The larva is a Prionine type, and most differences from Prioninae (chiefly extensive asperities and a tendency of prothoracic sternellar fold to fuse with the mesosternum) are clear apomorphies. The idea of *Parandra* being the most primitive Cerambycid, or even a linking element with the Cucujoidea, must be abandoned. The unusual adult appearance, as well as the ± pentamerous tarsus with reduced ventral pads, should be probably ascribed to the somewhat unusual adult habits (see bionomics of Parandrinae). The fourth tarsal segment might well have been exposed simply by reduction of the lobes of the third segment. All these tarsal modifications may be connected with the leg adopting some new functions and losing to some extent the walking function, which is clearly the case in *Spondylis* (see below). I see little sense in separating from Cerambycidae e.g. of the genus *Distenia* with its typical cryptopentamerous padded Cerambycid-like tarsus, and at the same time considering the pentamerous tarsus of *Parandra* to be primitive (LINSLEY, 1962a). As far as larvae are concerned, the genus Parandra seems to have certain affinities towards the Prionine tribe Macrotomini.

The genus *Apatophysis* has no direct relation to the Lepturinae, and it has been placed in a separate subfamily Apatophyseinae (DANILEVSKY, 1979b). It is undoubtedly related to Cerambycinae.

Despite DUFFY (1957, 1980), the genus *Dorcasomus* can be on no account retained in Lepturinae, and, although differing in some characters from *Apatophysis,* it should be provisionally included in the Apatophyseinae (see chapter on problematic larval forms). The writer suspects all the Lepturine-like forms occurring in the Ethiopian Region (incl. Madagascar) to be of a similar taxonomic position (I have seen some indetermined adults from Madagascar extremely similar to the genus *Apatophysis*). The only one true Lepturine species known to me from the Ethiopian Region, namely *Apiocephalus punctipennis* from East Africa, has clear Oriental affinities (after all, some authors treat East Africa as a transitional region between Oriental and Ethiopian Realms). Thus it might well be found that the Ethiopian Region essentially lack Lepturinae, and then the latter subfamily would become pronouncedly Holarctic, with outsprings in the Oriental and Neotropical Regions. (Lepturinae are absent from the Australasian Region, the genus *Blosyropus,* once treated as a member of the latter subfamily, has a Cerambycine larva.)

On the other hand, the North American genus *Desmocerus* is a true Lepturine with no relations to *Dorcasomus*. Separating of the tribe Desmocerini against all other

Lepturinae (LINSLEY et CHEMSAK, 1972) seems questionable, the larva of *Desmocerus* showing certain affinities to some other Lepturine genera, e.g. *Pseudogaurotina.* The North American genus *Centrodera,* occasionally considered related to *Apatophysis* (GRESSIT, 1951), is a true Lepturine, belonging into the tribe Xylosteini (larvae of *C. decolorata* at my disposal).

Authors studying Cerambycid larvae have already noted (CRAIGHEAD, 1923; DUFFY, 1953) that the subfamilies Lepturinae and Aseminae are problematic as long as the tribe Necydalini being included in the former. The larvae of the latter tribe show approximately equal affinities towards the two above subfamilies. However, joining of Aseminae and Lepturinae might result in the necessity to join Prioninae and Parandrinae into one subfamily and all other Cerambycidae into another one, as it cannot be excluded that some Aseminae might be closer to the Lamiinae, or to the Cerambycine stock, than to any Lepturinae. This two-subfamilies concept, although perhaps correct, would stand sharply against the more-subfamilies concepts of recent taxonomists, and the problem would be only postponed to the next lower taxonomic level, so we have chosen the other alternative, namely raising Necydalinae to the subfamily rank.

As there have been often problems with distinguishing between adult Aseminae and Cerambycinae, I am listing the world genera definitely known to have Asemine larvae: *Pectoctenus, Alocerus, Schurmannia, Saphanus* (incl. *Drymochares*), *Michthisoma, Oxypleurus, Anisarthron, Atimia, Paratimia, Vandykea, Nothorhina, Tetropium, Spondylis, Asemum, Megasemum, Arhopalus* (incl. *Cephalallus* and *Cephalocrius*). I have personally seen larvae of all these genera. I suppose some other genera might join this list, but their larvae are unknown. On the other hand, such genera as *Hybometopia, Tetropiopsis, Blabinotus* and others (often once classified in the tribe Saphanini) have been proved to be Cerambycinae. For *Opsimus* see chapter on problematic larval forms.

The subfamily Spondylinae is a taxonomic error, the genus *Spondylis* (and undoubtedly also *Scaphinus,* but larvae unknown) belonging into Aseminae, Asemini. The unusual adult appearance caused by the partly subterranean habits (see bionomics of *Spondylis*). In addition, the larvae of the North American *Spondylis upiformis* differ considerably from those of the type species, *S. buprestoides* (see note in close of the *Asemum*-group).

The subfamily Lamiinae seems to present no problems regarding its definition. Even larvae of some questioned groups (e.g. the Australasian tribe Tmesisternini) have proved to be typical Lamiinae. The origin of the subfamily has been placed by many authors near to the Aseminae, and this opinion corresponds well with the larval morphology.

My present opinion regarding relations of individual subfamilies is shown in Fig. 1A. The area with the question mark indicates my complete uncertainity about relations of the four subfamilies, the Lepturinae, Necydalinae, Aseminae and Lamiinae.

Finally I would like to point out the great value of the study of larvae for higher classification of the family. Indeed, larvae have proved in many cases much more suitable for that purpose than the adults (the main larval disadvantage, i.e. the scarcity of collected larval material, will, I hope, diminish in the future). The reasons are not quite clear, but one of them should be the following.

Adult Cerambycids are usually free-living active animals whose external morphology (mostly used for the classification purposes) may be influenced by a great variety of environmental pressures. An idea seems to me justified for example that the sight--searching predators (e.g. birds, lizards) may represent one of the greatest dangers particularly for the day-active species (the widespread mimetism in many unrelated Cerambycid groups may serve as a proof). Correspondingly we find extreme morphological variability among adult Cerambycidae.

Now, it is obvious that the larvae are in a rather different position. It will be pointed out in the chapter on larval habits of the Cerambycidae that we know no truly free--living larvae. Their defence mechanisms against various enemies will therefore be mostly other than morphological (e.g. ethological), and the morphological adaptations will result mostly from the mode of life (which is not very scattered among Cerambycidae, and in some non-typical cases the larvae may be strikingly aberrant, too - I can remember e.g. some highly specialized subcortical Lepturinae, fig. 12E, or the C-shaped *Agapanthia* type of the Lamiinae adapted for moving in hollows of greater diameter than is the diameter of their own body). It seems therefore reasonable to suppose that the larvae will give an evidence about their relationship more readily than the adults. In other words, adult external morphological adaptations will conceal or pronouncedly falsify true genealogical relationship. If this is true, then the larvae should generally prove more advantageous for classification purposes than the adults, except for the species level (of course we should best consider all stages). Indeed, larvae of closely related species are frequently more or less indistinguishable from each other. I am a strict opposer to some concepts treating larva and adult as two ± independently evolving entities, based in my opinion on misinterpreted and overvalued genetic hypotheses of ± separate immature and adult genetic programmes. The larval and adult classifications can be undoubtedly correlated, there is only a greater »taxonomic hum« in the adult stage of the Cerambycidae.

KEY TO FAMILIES

Note: Before this key is used, the reader must go through the general morphology of the family Cerambycidae to get known with morphologic terms and their exact content in the present paper. Diagnoses of the other four families are given in many respects as differential ones, comparing them with the Cerambycidae, and, as well as the following key, they cannot be understood without knowledge of morphology of the latter family. General morphologic characteristic of the whole complex included in the present paper has not been made for one simple reason - it would be almost meaningless. I doubt that the group as presented here might represent a natural unit. The selection of the included families has been based on one single fact - whether the group has been recently considered a member of the family Cerambycidae. The purpose of the following key is therefore synthetic rather than analytic, i.e. it should serve as a short and comprehensive summary of principal differences rather than for determining the family (since there is also no general way how to find out if an unidentified larva belongs to any of those families at all, and each family must be treated independently in that respect). That is also why the key couplets are rather extensive and include also characters requiring thorough study, unsuitable for determination or not fully distinctive.

1(2) Clypeus normal, ± not separated from frons, strenghtened epistomal margin absent. Antennae very long, non-retractile, articulating on special separate cranial buds. Long exposed (or exposable) coronary suture present (Figs 2A, 2B). Dorsal and ventral intersegmental abdominal zones simple and meeting each other. Body very short and robust, pear-shaped (Fig. 1B). Abdominal terga and sterna with setal spines (Figs 2C, D), true ambulatory ampullae absent. [Gula absent, metatentorial bridge very broad. Labrum free (Figs 2A, 2B). Anus essentially transverse cleft.] . . . . . Vesperidae

2(1) Clypeus distinctly separated from frons by strenghtened epistomal margin, or sclerotized and fused with both frons and labrum. Antennae almost always shorter, always (particularly if they are long) deeply retractile, cranial articulating buds absent. Exposed coronary suture absent, dorsal head retractors attached on or immediately behind frontal base. Abdominal intersegmental zones more complex, dorsal and ventral ones do not meet exactly each other. Body ± elongate. Abdominal terga and sterna without spines of setal origin, at least some dorsal ambulatory ampullae present.

3(8) Gular bridge absent, submentum articulating directly with propraesternum. Metatentorial bridge very broad (Figs 3A, 4B, 5B).

4(5) Clypeus membraneous, with transverse row of stout setae. Posterior part of occipital foramen dorsal, frons medially extremely short, endocarina absent. Ligula deeply bilobed, praelabium protruding deeply into mentum (Figs 2G, 3A). Fore legs remarkably enlarged, abdominal segments 3 to 5 with ventral prolegs (Fig. 3B). [Labrum free, anus triradiate.] . . . . . Anoplodermatidae

5(4) Clypeus devoid of setae, or head with sclerotized nasale. Posterior part of occipital foramen at least posterodorsal, frons much longer, endocarina present. Ligula not bilobed, praelabium not protruding into mentum. Fore legs not enlarged, abdominal prolegs absent.

6(7) Clypeus and labrum sclerotized and fused with frons forming nasale. Cranium elongate, inner margins of epicranial halves running parallelly backwards very close to each other (Figs 4B, D). Anus triradiate, ventral radius very long and deeply bisecting anal segment . . . . . Oxypeltidae

7(6) Clypeus membraneous, labrum free. Cranium transverse, inner margins of epicranial halves diverging (Fig. 5B). Anus transverse cleft . . . . . Disteniidae

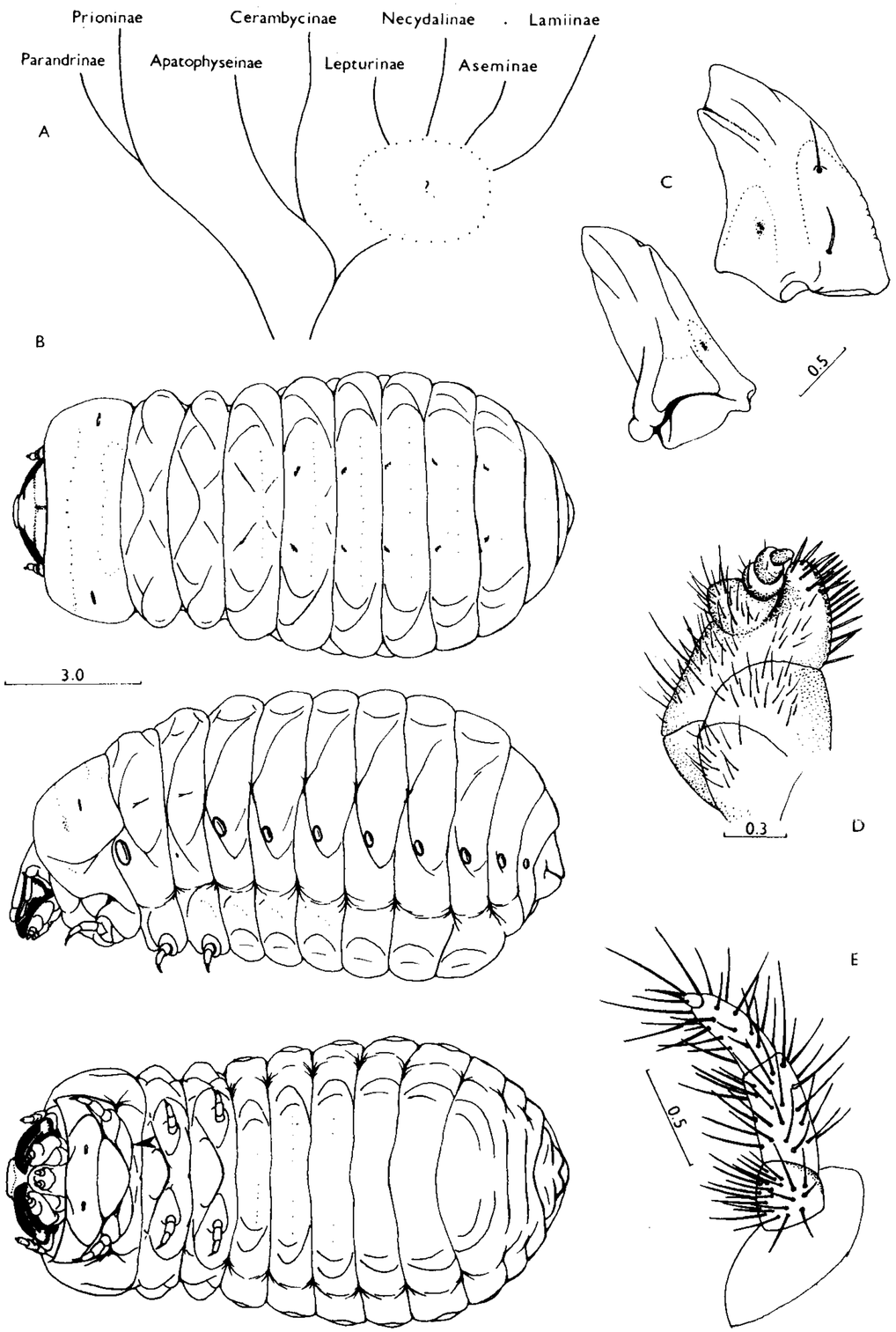
8(3) Hypostomal halves bridged by longer or shorter gula separating submentum from propraesternum. Metatentorial bridge narrower (Figs 6E, 7A to D). [Clypeus with at most lateral setae. Labrum free. Occipital foramen posterior to ventral. Ligula not bilobed. Fore legs not enlarged, abdominal prolegs absent.] . . . . . Cerambycidae

Family Vesperidae MULSANT, 1839

The family contains one genus.

Genus *Vesperus* DEJEAN, 1821

Type species: *Stenocorus strepens* F., 1792 (? VILLIERS design., 1974)



Body form quite dissimilar to any known Cerambycid - short, very robust, broadest behind (Fig. 1B), similar in shape to some Chrysomelid larvae. Body white or yellowish, almost unsclerotized, bearing ± numerous setae.

Head (Figs 2A, 2B) in natural position partly retracted (but may be almost entirely exposed), almost orthognathous (mouthparts pointed obliquely ventrad), basically different from all Cerambycidae. Cranium subquadrate (about 1.3), moderately depressed (about 1.8 – 1.9), only moderately sclerotized, mouthframe not remarkably strenghtened. Long free coronary suture present, main head retractors attached at hind cranial margin, cranium lacking doubled concealed region of most Cerambycidae. Coronary line infolded, forming a low internal carina. Epicranium with distinct dorsal longitudinal row of miniature setae on each side. Frontal lines rather indistinct (more so in *V. xatarti*) particularly in anterior halves, cleavage line apparently running below antennae (no exuvia available). Transfrontal line absent. Frons ± transversely rugose, bearing various number of setae. Endocarina present, vanishing without reaching clypeus. Postcondylar carinae absent. Anterior frontal ,margin with transverse row of at least four setae. Frons passing smoothly into clypeus no epistoma, strenghtened epistomal margin or even a distinct border line present. Dorsal mandibular articulation lies in angle between lateral clypeal margin and anterior frontal margin. Clypeus very large, long, trapezoidal, indistinctly divided into posterior slightly sclerotized postclypeus and anterior ± membraneous anteclypeus, with two groups of setae between latter two areas on each side, and with one pair of broad shallow sclerotized pits. (The setae may be homologous with the epistomal setae of the Cerambycidae.) Labrum transverse, with two discal and very sparse marginal stout setae. Epipharyngeal setae reaching far behind, tormae very short, triangular, hind epipharyngeal part not raised, finely sclerotized along sides. Pleurostoma and gena ± not distinguished, anterior cranial margin between dorsal and ventral mandibular articulations only very narrowly finely sclerotized, with short blind oblique branch about middle (Fig. 2B). Three small pigmented spots of main stemmata in vertical row visible under cuticle behind antennae, in mature larvae may be ± indiscernible. Gula and hypostomal lines absent. Metatentorial bridge very broad, occupying most of ventral cranial wall, with only narrow space left below submentum (nerve cord leaves cranial cavity through this space which corresponds with anterior part of »divided« occipital foramen of some Cerambycidae). Hind part of occipital foramen small, posteroventral (posterior if the head is in natural oblique position). Metatentorium invaginated from border between cranium and postcranial membraneous region, metatentorial pits therefore absent.

Plate 1: A – Possible cladistic relationship of subfamilies of Cerambycidae. B – *Vesperus xatarti*, submature larva, dorsal (upper), lateral (middle) and ventral (lower) views. (The arrow in the lower figure marks the point of invagination of prothoracic furca. Setae not figured.) C – *V. strepens*, later instar, right mandible, dorsal (upper) and medial (lower) views. D – *V. xatarti*, half-grown, right maxilla with connecting lobe, ventral and slightly medial view. E – *V. xatarti*, later instar, left fore leg, posterolateral view. (Coxal setae not figured.)

Antennae (Fig. 2A) very long, three-segmented. Sclerotized basal ring absent, antennae articulating on special separated basal pieces of cranial origin. (These setose structures must not be confused with the connecting antennal membrane of the following four families which is, among other, always essentially glabrous. The connecting membraneous region of Vesperus is very small, enables necessary moving of the antenna but does not allow almost any retraction characteristic for all the four following families.) First two segments slender, elongate, sclerotized, third segment very small, moderately elongate (*V. xatarti,* all four available larvae of *V. strepens* have this segment broken). Main antennal sensilla on apical face of second segment flat, elliptical (usually slightly curved) in apical view. Mandibles (Fig. 1C) differ from all types found in Cerambycidae, similar to certain other beetle families; symmetrical, long, slender. Apical part strongly sclerotized, dark, flat, shovel-like, cutting edge sharp, simple, dorsal angle separated by a notch, dorsal face with a ridge running from dorsal angle backwards. Inner face of apical part flat, with two low ridges running towards apex and one indistinct ridge at dorsal angle. Lateroventral edge very sharply carinate along whole mandible. Basal part moderately sclerotized, at least partly pale, molar part simple, lateral face ± transversely to irregularly rugose, bearing two setae, ventral one moved far anteriorly. Labiomaxillary complex robust, more retracted in comparison with Cerambycidae. Basal areas well defined, finely sclerotized, submentum bearing two setae, connecting lobe large, divided by deep transverse furrow in two lobes, both of them bearing setae. Cardo large, free, movable. Stipes and palpiger feebly sclerotized (former without basal pigmented band typical for most Cerambycidae), bearing numerous stout setae. Palpiger process absent. Mala moderately broad, with sharply carinate inner side bearing very few extremely stout lanceolate setae (Fig. 1D). Maxillary palps three--segmented, sensory area of third segment small, apical. Mentum moderately sclerotized at base, praelabium comparatively small, labial palpigers almost unpigmented, ligula very small, reduced, both ligula and palpigers bearing dense stout setae. Palps two-segmented, close to each other. Dorsal (hypopharyngeal) part unsclerotized, hypopharyngeal sclerome absent. Sclerotized hypopharyngeal bracon absent.

Prothorax moderately large, most of it covered with numerous short setae. Protergum ± undivided (lateral furrows absent), almost without anterior pigmentation, medial cleavage line rather distinct. Epipleural fold completely delimited, tapering anteriorly, divided by deep oblique impression in two lobes. Episternum and epimeron defined, former with anterior angle membraneous, distinctly distinguished from remaining finely sclerotized area (this anterior angle evidently does not belong to true episternum and has been attached to it later, both here and in other Coleoptera incl. Cerambycidae). Prothoracic sternum quite different from Cerambycidae. Coxae defined, coxosternum non-developed, basisternum large, prominent, sternellum reduced, membraneous. Coxae posteromedially with another adjacent separate unnamed region. Prothoracic endoskeleton present (broad pleural apodeme, robust spina and slender paired furca invaginated at hind border of above mentioned

unnamed region (Fig. 1B). Praesternum relatively smaller than in Cerambycidae, divided in posteromedial and anterolateral parts (non-homologous with medio- and lateropraesternum of Cerambycidae), posteromedial region with two sclerotized spots or shallow broad pits. Anteriorly praesternum joined through membrane directly with labiomaxillary base.

Pterothorax: Praescutum well separate, scutellum indistinct, scutum I not very conspicuous. Laterally scutum separated by deep oblique furrow and a shallow impression from alar lobe. Mesothoracic spiracle elliptical, moderately sclerotized, slightly protruding into prothorax. Marginal chambers absent. Rudimentary metathoracic spiracle well visible. Praesternum extremely reduced. Pleurum undivided (pleural sulcus and pleural apodeme absent), large, broadly separating epipleurum from coxa; latter well defined, large, transverse. Basisternum large, prominent, sternellum reduced, membraneous. Some regions of pterothorax (and to smaller extent also of some other body segments) very abruptly protuberant (e.g. scutum, alar lobes, pleurum, basisternum), particularly in *V. strepens.* Mesothoracic spina and furca present, latter, however, moved to hind mesothoracic margin and ± levelling with spina. Metasternal endoskeleton absent.

Legs rather well developed, full number of segments of Polyphaga-leg, all segments well defined. Fore legs somewhat larger and pointed more anteriorly, otherwise similar to meso- and metathoracic legs. Trochanter, femur and tibiotarsus bearing numerous setae, trochanter about as long as broad, femur and tibiotarsus elongate, cylindrical. Praetarsus slender, conical, bearing one seta from inner side, claw needle--shaped, sclerotized (Fig. 1E).

Abdomen: True ambulatory ampullae absent. Border zones between neighbouring abdominal segments continuous, simple, dorsal and ventral intersegmental lines meet each other (dorsal part not moved forward in comparison with ventral one), abdomen much less movable than in following families. Segments 1 to 6 well developed, with large flat dorsal and ventral plates with numerous setae, some of which are modified, forming sharp stout spines (Figs 2C, D) - these spines are basically different from microscopic spines of Cerambycidae which are of non-setal origin (in *Vesperus,* such spines are also present on some membraneous body areas). Abdominal nota 1 to 6 consisting of large ± entire medial plate and two separate lateral lobes on each side, perhaps homologous with parascutum of Cerambycidae. Medial plate without any distinct transverse lines; unlike in Cerambycidae, abdominal terga having much in common with those of pterothorax. Particularly first abdominal tergum bearing distinct rudiments of praescuto-scutal line (Fig. 1B), and lateral one of two separate side lobes also seems to be homologous with lateral ± separate scutal lobe of pterothoracic segments (in abdomen this lobe fused with spiracular area). Spiracles on segments 1 to 8, much smaller than mesothoracic one, otherwise similar. Epipleurum moderately protuberant on segments 1 to 8, pleural tubercle not sharply defined (although epipleurum particularly in *V. strepens* with distinct protuberance). Venter of segments 1 to 6 consisting of large ± entire medial plate (transsternal line almost

absent) followed laterally by coxal and less prominent pleural lobes. Medial plate bearing setal spines similar to dorsal plate. Sixth sternum enlarged and modified (Fig. 1B), with right and left impressions separating coxal lobes connected by curved transverse line along hind margin. Abdominal segments 7 to 10 very much reduced, ± entirely membraneous, in living larvae more or less telescoped making abdomen truncate posteriorly. Segments 9 and 10 particularly strongly reduced. Caudal armature absent. Anus in form of transverse cleft, its lower lip with only very fine shallow medial impression.

The genus *Vesperus* is distributed in the Mediterranean area, both in Europe and North Africa. Larvae of two species at my disposal:

1(2) Setae (incl. dorsal and ventral abdominal setal spines) denser, finer (Figs 2A, D) . . *xatarti*
2(1) Setae incl. setal spines sparser, stouter (Figs 2B, C) . . . . . *strepens*

Vesperus xatarti DUFOUR, 1839

Setae dense, relatively finer. Frontal lines rather indistinct. Stemmata in mature larvae ± indiscernible. All body areas only moderately protuberant. Largest available larva 23 mm.

Habits: Larvae terricolous, feeding on roots of various plants, often reported from *Vitis*. Several-year development, pupation in soil.

Distribution: Spain, France (Pyrenées Orientales).

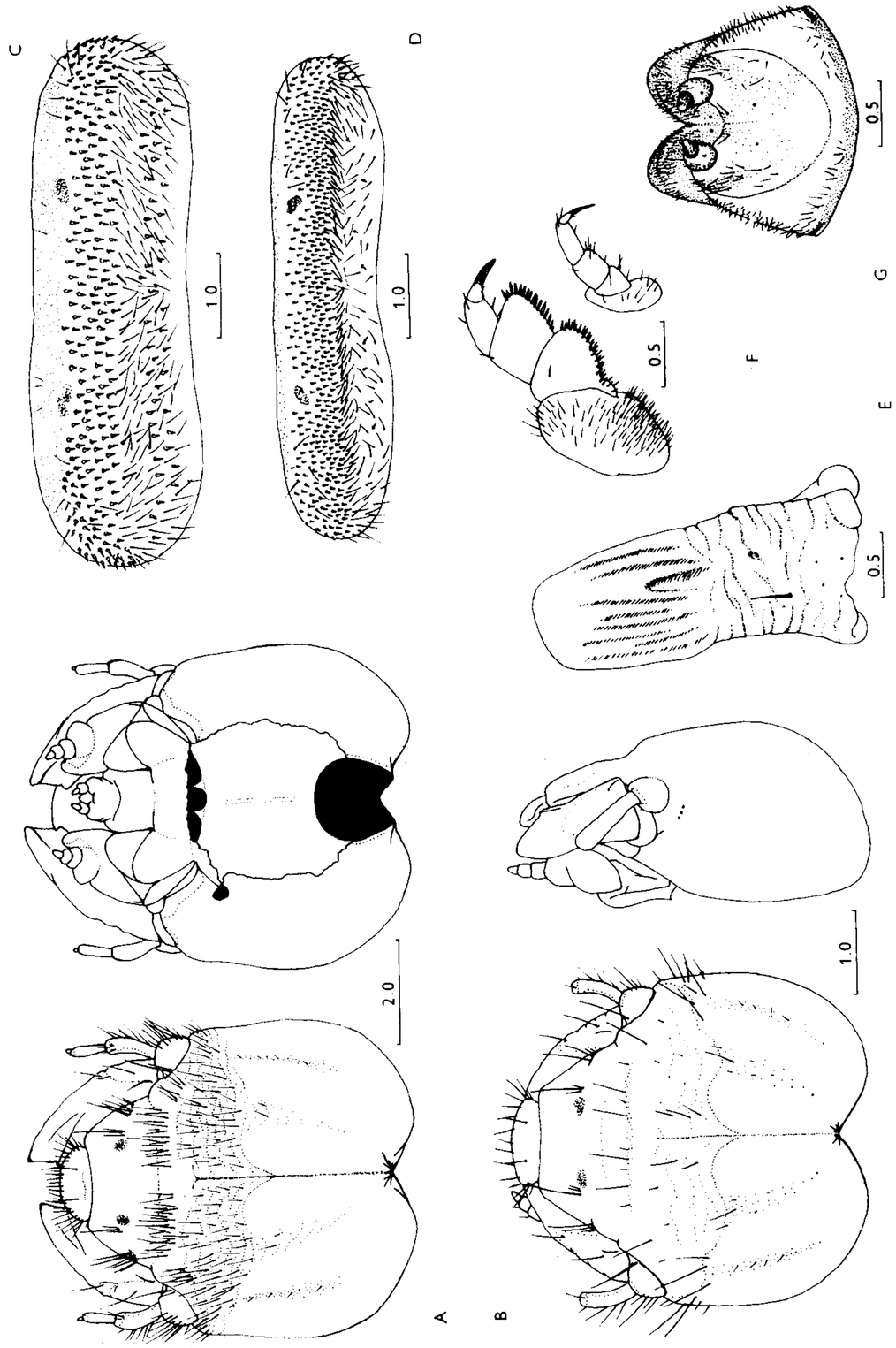
Material: 15. 7. 1959 France, Pyr. Or., Banyuls-sur-Mer, 2/?, in soil at roots of *Celtis*, R. A. Crowson lgt., coll. British Museum; V. 1978 Spain, Albacete, Puerto de las Crucetillas (1 700 m.), 2/?, under stones, G. Sama lgt., coll. S; 19. 4. 1974 Spain, Alcoy, La Carrasqueta, 1/—, E. Vives lgt. et coll; 21. 3. 1980 Spain, Teruel, 1/?, E. Vives lgt. et coll; France, Pyr. Or., 1/—, Schaefer lgt., coll. M. Sláma.

Vesperus strepens (F., 1792)

Setae remarkably sparser, stouter. Frontal lines more distinct, three minute yet distinct pigment spots of main stemmata present in all available larvae. Certain body areas (notably mesothoracic alar lobes, basisternum and others) sharply abruptly protuberant. Largest available larva 20 mm.

Habits apparently similar to the preceding species. OLMI (1974) described grave infestation of a vineyard in Italy.

Plate 2: A — *Vesperus xatarti*, mature, head, dorsal (left) and ventral (right) views. (Setae rather dense in this very large specimen, usually slightly sparser; they are not figured in the ventral view.) B — *V. strepens*, later instar, head, dorsal (left) and lateral (right) views. (Setae figured only in the dorsal view.) C — *V. strepens*, mature, third abdominal tergal plate. D — *V. xatarti*, later instar, dtto. E — *Migdolus fryanus*, later instar, right mandible, lateral view. F — *M. fryanus*, later instar, right fore leg, lateral view (left), and right middle leg, posterior view (right). G — *M. fryanus*, later instar, distal labium (mentum and praelabium), anteroventral view.



Distribution: Italy, France (Provence).
Material: V. 1977 Italy, Albenga (Savona), 4/I, in soil, M. Olmi lgt., coll. S.

Family Anoplodermatidae GUÉRIN-MÉNÈVILLE, 1840

Exclusively Neotropical family. Larvae of one single genus known.

Genus *Migdolus* WESTWOOD, 1863

Type species: *Migdolus fryanus* WESTWOOD, 1863 (monobasic)

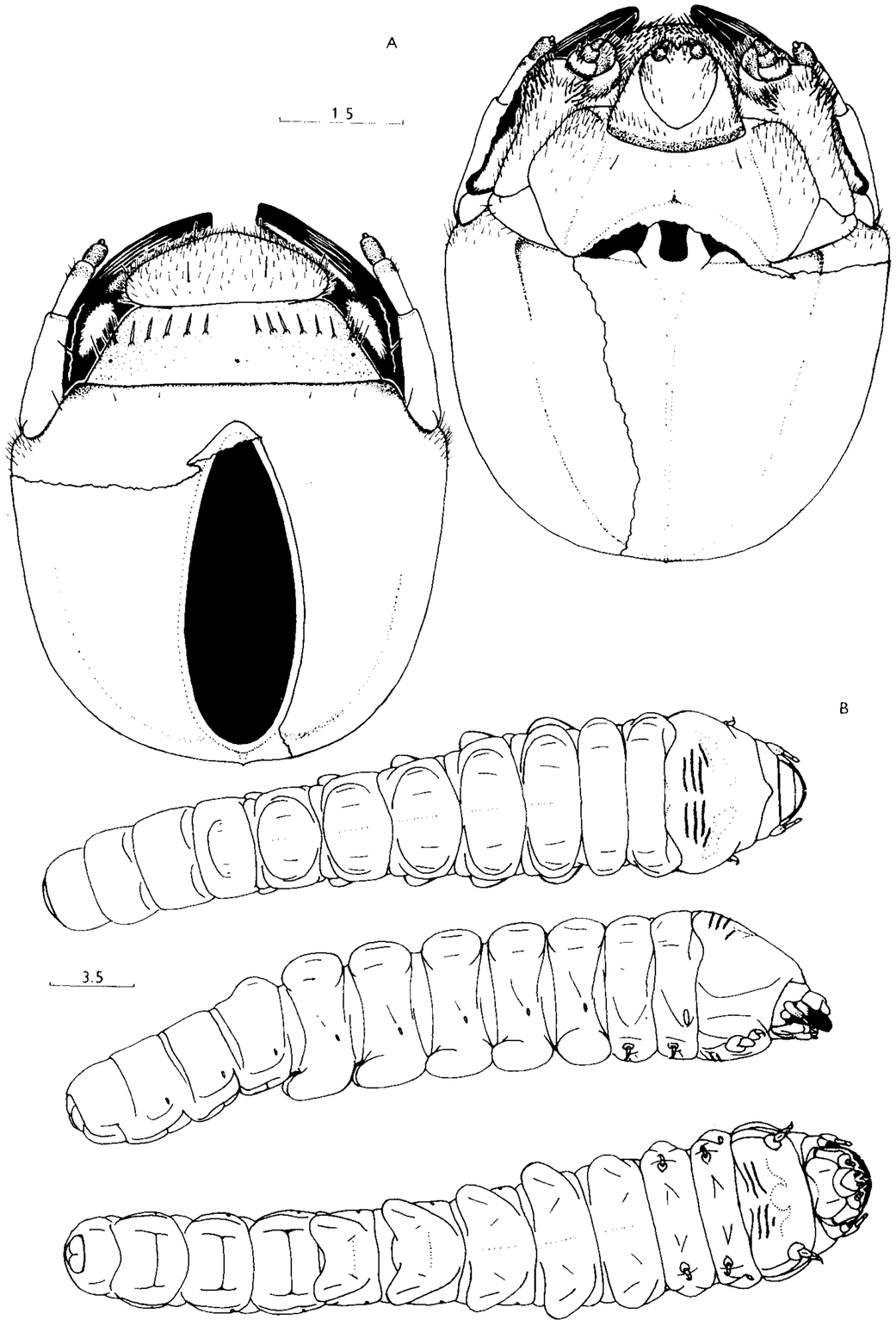
Body (Fig. 3B) white, unsclerotized, moderately elongate, almost not depressed, ± tapering posteriorly, bearing sparse minute pale setae with remarkable exception of prothorax which is almost entirely covered with similar but very dense setae (Fig. 4A).

Head prognathous, very deeply retracted, cannot be exposed except for short anterior part, large posterior part cemented to inner surface of prothoracic pocket. Cranium subquadrate (1.16), moderately depressed (1.89; one specimen measured), moderately tapering posteriorly, ± smooth, feebly sclerotized, almost unpigmented except for small spots at dorsal and ventral mandibular articulations and very narrow lateral and lateroventral margin. Frontal lines indiscernible, cleavage lines unknown (exuvia not available). Dorsal doubled cranial region non-developed, coronary suture absent, dorsal part of occipital foramen deeply protruding into frontal region, frons medially extremely short (Fig. 3A). Endocarina (and consequently medial frontal line) absent. Postcondylar carina absent. Anterior frontal margin (although unpigmented) of structure similar to Cerambycidae - frontoclypeal border sharp, infolded and sclerotized, making anterior frontal margin transversely strenghtened (calling this margin epistomal seems therefore justified). Separate epistoma absent. Cranium laterally with short fine setae at anterior margin, a few minute setae also along epistomal margin (perhaps homologous with epistomal setae of Cerambycidae), otherwise cranium glabrous. Clypeus short, trapezoidal, ± unsclerotized, with transverse row of stout thin-walled setae pointed forward. Labrum transverse, flat, unpigmented, bearing very short pale marginal and scattered discal setae. Epipharynx anteriorly with similar but much denser setae and a medial group of sensilla of varying size, small ones arranged in ± distinct transverse row. Hind part poorly raised, covered with fine dense microtrichia excepting smooth medial band. Tormae short, ± transverse. Pleurostoma and gena not distinguished from epicranium. Very narrow sclerotization of lateral anterior cranial margin interrupted below antenna (apparently otherwise invisible frontal lines reaching anterior cranial margin). Subfossal process and stemmata absent. Gula absent, short yet distinct hypostomal lines present. Metatentorium extremely hypertrophied, occupying entire medial region of ventral cranial face. (It is difficult to draw exact border line between metatentorial and hypostomal regions because of the

whole hind cranial part firmly attached to the inner surface of the prothoracic pocket.) Anterior margin of metatentorial plate (in addition to usual thin anterior metatentorial arms leading inside cranial cavity) with two auricle-shaped processes (Fig. 3A). Hind part of occipital foramen (behind metatentorial bridge) pushed entirely on dorsal cranial face, stomodaeum of very characteristic shape, with short blind ventral branch before leaving cranial cavity.

Antennae extremely long, three-segmented; regardless of their length they may be almost completely retracted into cranium owing to very large connecting membrane (Fig. 3A showing them fully protracted). Antennal ring very narrowly sclerotized, not raised. First segment very long, almost completely desclerotized except for narrow incomplete subapical ring. Second segment sclerotized, slightly longer than broad. Third segment minute, main antennal sensilla slightly projecting, very shortly conical. Mandible (Fig. 2E) long, slender. Apical part strongly sclerotized, apex and dorsal angle blunt, very close each other, dorsal and ventral edges broadened, extended, sharply carinate, apical part ± quadrangular, spade-shaped. Outer face roughly longitudinally striate, inner face with two very indistinct low ledges running towards ventral apical angle and one towards dorsal angle. Basal part feebly sclerotized, some regions almost unpigmented. Molar part simple, dorsoventrally depressed, outer face roughly transversely rugose, bearing only one seta (dorsal one of two setae of other families). Labiomaxillary complex large, robust. Basal components well separate, submentum large, emarginate posteriorly, connecting lobes large, divided by at most shallow fine transverse impression, cardo large, free, unpigmented, bearing several short setae. Stipes unpigmented, large, partly covered by connecting lobe. Palpiger separated only by lateral notch, ventral face protuberant and bearing rather stout setae, process absent. Palp short, stout, three-segmented, segments moderately sclerotized. Mala relatively small, with short pigmented band and sharp flattened inner edge. Mentum with narrow basal transverse continuous pigmented band. Praelabium protruding deeply into mentum, labial palpigers ± not distinguished, palps short, two-segmented, moderately sclerotized. Ligula and whole dorsal labial part unsclerotized, very deeply medially impressed, divided in two separate longitudinal lobes, each lobe anteriorly with short dense setae (Fig. 2G). Hypopharyngeal bracon absent.

Prothorax moderately large, almost entirely covered with minute dense pale setae. Pronotum not separated from alar lobes, lateral furrows absent. Anterior pigmented band ± absent. Posterior half of pronotum with several raised sclerotized ridges of somewhat unstable arrangement, they are interrupted by medial longitudinal cleavage line. Pronotum expanded backwards, somewhat reducing mesonotum. Ventral margin of alar lobe forming separate longitudinal fold above epipleurum, latter in form of another simple longitudinal fold. Venter strongly modified, all parts ± fused, fore legs moved far forward, coxa rounded, sharply delimited. Sternal region posteriorly with sclerotized ridges similar to those on pronotum. Prothoracic endoskeleton present; short spina, furca reduced, its arms short, broadly



separate from each other, arising from hind prothoracic margin ± at same level with spina (deep impressed lines originate from that point, separating narrow posterior sternal region behind ridges - Fig. 3B). Pleural apodeme arising at anterior coxal margin, pointed obliquely backwards, long, slender, almost reaching furcal arm of its side. Some fine membraneous regions of prothorax covered with dense fine microscopic spines.

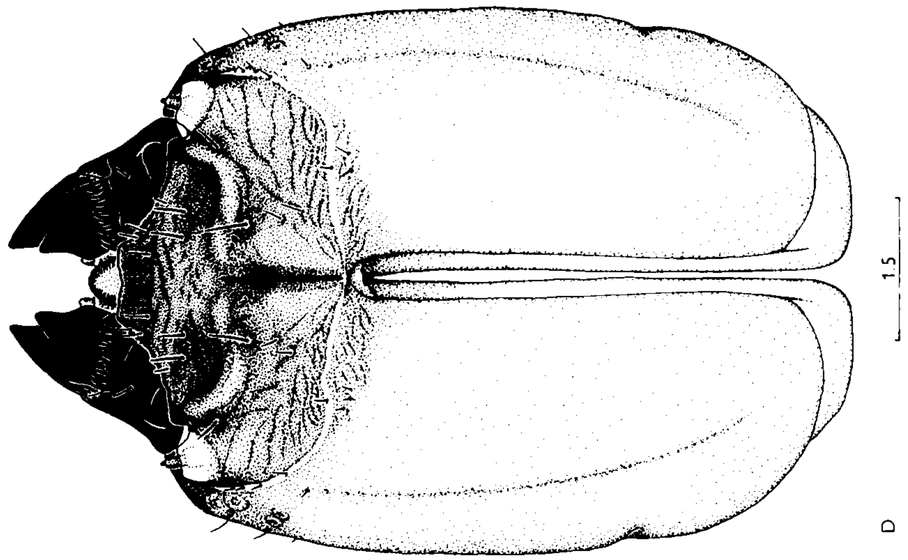
Pterothorax and abdomen entirely membraneous, almost completely finely microspiculate.

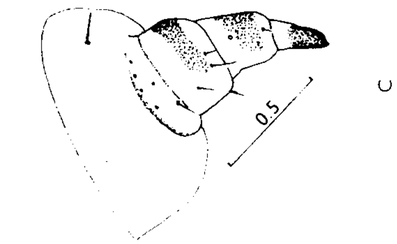
Mesonotum shorter than metanotum, reduced by expanded pronotum. Metanotum divided by fine X-shaped lines, in mesonotum they are rather indistinct. Postnotum non-developed. Scutum I of metathorax indistinct. Lateral parts of scuta separated by short longitudinal impressions. Alar lobes not protuberant. Mesothoracic spiracle moderately large, elliptical, not protruding into prothorax, marginal chambers absent. Spiracle-bearing epipleural area ± fused with alar lobe. Rudimentary metathoracic spiracle very small yet well discernible. Epipleurum broad, pleurum narrow, episternum and epimeron ± separate, in that point pleurum strongly constricted (mesothoracic coxa almost touching epipleurum). Praesternum extremely reduced. Coxa extremely small, well defined. Transsternal line indistinct, almost absent on metasternum, basisterna divided by oblique impressions. Pterothoracic pleural and sternal endoskeleton absent except for rudimentary mesothoracic spina.

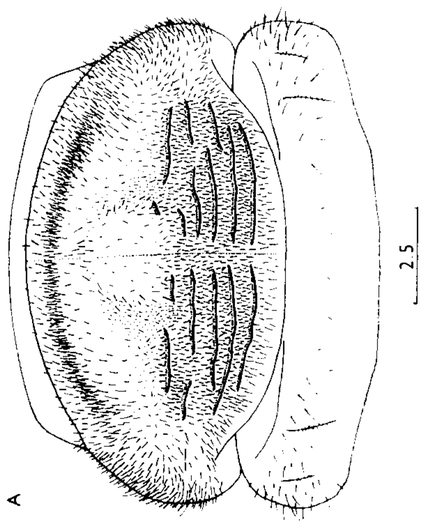
Fore legs remarkably enlarged (Figs 2F, 3B), moved far forward, perhaps adapted for digging, pointed obliquely forward. Trochanter and femur somewhat flattened, with carinate ventral faces bearing row of short very stout setae. Trochanter as large as femur. Tibiotarsus small, cylindrical, almost glabrous. Praetarsus strong, tooth-shaped, almost entirely sclerotized, may inconstantly bear minute seta at base. Pterothoracic legs much smaller, slender, unmodified, similar each other, praetarsus with at most miniature seta.

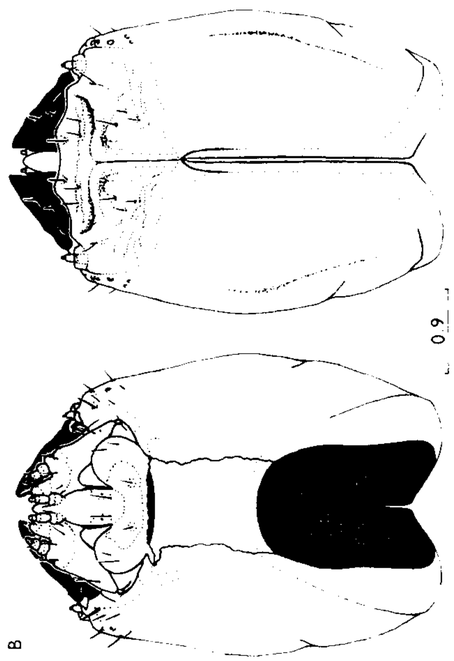
Abdomen uniquely modified. Segments 1 to 5 must be treated separately from others: Dorsal ambulatory ampullae present (much smaller ampulla present also on segment 6), each with two longitudinal impressions on each side, transverse lines almost fully obliterated. Parascutum almost not separated from spiracular area. Spiracles similar to mesothoracic one, much smaller. True dorsal epipleural border rather indistinct, most of epipleurum taking part in building up curious ventral pseudopods (initial on first segment, well developed on segments 2 to 5). In these pseudopods are also involved pleural and partly coxal lobe. Each pseudopod at its extremity (!) with rounded area of very fine cuticle with central pit - perhaps some structure homologous with Cerambycid pleural discs. Each pseudopod on ventral side with oblique impression (ventral epipleural boundary), borders of pleural and coxal lobes rather indistinct, transsternal line absent.

Plate 3: A — *Migdolus fryanus*, later instar, head, dorsal (left) and ventral (right) views. (Membraneous »pocket« not removed on the left side.) B — *M. fryanus*, half-grown larva, dorsal (upper), lateral (middle) and ventral (lower) views. (Setae not figured.)









Sixth and following abdominal segments quite different. Terga simple except for segment 6 bearing small ampulla (surface of all six dorsal ampullae, as well as of ventral pseudopods, almost not distinguished from other abdominal surface except for microscopic spines slightly more distinct). Spiracles as in segments 1 to 5 (all 8 abdominal spiracles present). Epipleurum of segments 6 to 9 abruptly protuberant, pleural tubercles or discs absent. Venter simple, coxal and pleural lobes not defined, segments 6 to 8 with fine transverse line extending from left to right epipleural folds. Caudal armature absent. Anal segment terminal, very short, almost not projecting from segment 9, anus triradiate, surrounded by three anal papillae. Intersegmental abdominal area arranged differently from Cerambycidae, abdominal terga (esp. 1 to 5) not moved forward in comparison with sterna. Intersegmental lines behind metathoracic and first five abdominal segments broadly doubled on each side, inclosing large separate lateral area.

Length (according to FONSECA, 1959) up to 50 mm.

Migdolus fryanus WESTWOOD, 1863

These larvae were described by FONSECA (l. c.) as belonging to *M. morretesi* LANE, 1937. Later on, they were assigned to a new species, *M. fonsecai* LANE, 1972. This species has been recently synonymized with *M. fryanus* (see DIAS, 1984).

Habits (FONSECA, l. c.): The terricolous larvae were found in light soils with fine particles feeding on roots of various plants, occasionally harmful to some cultural plants (sugar-cane - - *Saccharum, Eucalyptus*). Larvae usually eat out deep longitudinal grooves on the surface of thinner living roots, the plants may be seriously damaged or killed.

Material: 9. 11. 1954 Brazil, Piracicaba (Sao Paulo), five larvae ex coll. Instituto Biológico Sao Paulo, coll. S; three larvae in coll. of British Museum labelled »Migdolus morretesi Lane, Brazil, J. P. Fonseca leg.« (B. M. number 1962−2).

Family Oxypeltidae LACORDAIRE, 1869

Exclusively Neotropical group, two genera in Chile and Argentina.

Body (Fig. 5A) robust, ± parallel-sided, non-depressed, white, bearing very sparse minute setae.

Head (Figs 4B, D) narrow, very deeply retracted, prognathous. Cranium elongate, parallel-sided, depressed (about 2.2), mouthframe and frons strongly sclerotized. Exposed coronary suture absent, dorsal head retractors attached at frontal base. Epicranial halves very long, touching ± in one point, but their very long inner dorsal margins running parallelly backwards very close together (at first sight they seem to be fused along whole length similarly to Cerambycidae Lamiinae, as the

Plate 4: A — *Migdolus fryanus*, later instar, pro- and mesothorax, dorsal view. B — *Oxypeltus quadrispinosus*, head, dorsal (right) and ventral (left) views. (Posterior area of the metatentorial bridge of the single available larva damaged, the hind edge of the bridge hypothetical, may be slightly more, or slightly less emarginate than figured.) C — *Cheloderus childreni*, left middle leg, anterior view. D — *C. childreni*, head, dorsal view.

very narrow medial space is filled with soft tissue which can be, however, removed by a needle). Although very deeply retracted, hind cranial part not cemented to prothoracic pocket. Epicranium with darker longitudinal dorsal line on each side, anterior epicranial setae very short and sparse, dorsal longitudinal rows present but reduced, incomplete, inconstant. Frontal lines distinct, meeting each other at almost 180°, anteriorly passing below antennae, almost reaching anterior cranial margin, not entering antennal openings. Frons entirely sclerotized, roughly rugose, with one particularly abruptly raised medially interrupted transverse elevation whose lateral extremities curved forward towards dorsal mandibular articulations, and with broad fovea before that elevation. Endocarina present, medial frontal line distinct. Transfrontal line and postcondylar carina absent. Clypeus and labrum entirely heavily sclerotized, fused with each other and with frons, forming trapezoidal nasale, its lateral margins fringed with fine dense microtrichia. Setae as figured, it is not clear which ones (if any) are homologous with Cerambycid epistomal setae. Protentorial pits (indiscernible in other four families) unusually distinct between antenna and dorsal mandibular articulation. Pleurostoma heavily sclerotized, raised (particularly at ventral mandibular articulations), subfossal process absent, ± distinct blunt short longitudinal elevation running from ventral articulation backwards. Gena ± not distinguished from epicranium. Six stemmata on each side in generally similar position as in Cerambycidae (Figs 4B, D), dorsal main stemma distant from contiguous ventral two main stemmata. Hypostomal lines present, gula absent, metatentorial bridge very broad, lying in ventral cranial plane, metatentorial pits absent.

Antennae moderately long, slender, three-segmented. Antennal opening large, connecting membrane very large, smoothly passing into cranial cuticle, raised antennal ring absent, antennae deeply retractile. Segments 1 and 2 elongate, cylindrical, sclerotized, third segment small, main sensilla small, prominent, conical. Mandible short, robust, entirely strongly sclerotized. Apical part relatively small, outer face smooth, apex separated by short incision from posterior part of cutting edge which may be shallowly divided in two flat teeth. Inner face with two low ridges reaching apex, one short ridge below hind part of cutting edge. Basal part very robust, molar region large, quadrangular, not dorsoventrally flattened, similar to Cerambycidae. Two lateral setae borne from broad pits. Labiomaxillary complex more retracted than in Cerambycidae, moderately large, bearing very sparse setae. Connecting lobe sharply divided in two parts, posterior one much larger, ± fused with submentum, whole region largely sclerotized. Posterior part of connecting lobe partly covering cardo and stipes, former large, free, sclerotized, bearing short lateral seta. Stipes long, sclerotized except for distal margin, palpiger in ventral view separated only by indistinct lateral notch, process absent. Palps short, stout, three-segmented, segments sclerotized. Mala moderately broad, with short ventral pigmented band, inner face carinate, with dense microtrichia, only very few apical and subapical setae present. Mentum fused with submentum, sides finely pigmented. Praelabium gracile, labial

palpigers defined, sclerotized, palps two-segmented, ligula narrow, devoid of setae, covered with dense short microtrichia proceeding far backward along sides of dorsal labial part, latter very narrow, at most very finely sclerotized, hypopharyngeal sclerome and hypopharyngeal bracon absent.

Prothorax moderately large, tergum very tough, lateral furrows very feebly indicated at hind margin, alar lobes partly divided by longitudinal impressions in hind half. Protergum with broad anterior medially interrupted pigmented band with one notch on each side. Pronotum posteriorly ± rugose, with distinct medial line which in hind half becomes slightly infolded furrow. Epipleural fold markedly sclerotized, broadening anteriorly (anterior ventral boundary secondary). Pleurum defined, pleural sulcus indistinct. Coxal region poorly separated from, or fused with narrow medially constricted (interrupted) posterior sternal fold, all other sternal parts fused into one large anterior ± sclerotized plate (exact homologies unclear, the limited material does not allow dissections). Sternal and pleural endoskeleton absent except for rudimentary spina.

Small lateral regions of meso- and metanotum separated, otherwise mesonotum ± undivided, metanotum with two indistinct transverse lines. Postnotum non--developed. Alar lobes gently protuberant, mesothoracic spiracle not protruding into prothorax, small, narrow oval, with two small inconspicuous marginal chambers at upper extremity. Rudimentary metathoracic spiracle distinct. Pleurum large, broadly separating coxa from epipleurum, undivided. Praesternum extremely reduced. Coxae not very well defined, mesosternum with ± distinct transsternal line, metasternum with two transverse lines (anterior one more distinct).

Legs (Fig. 4C) very short, slightly longer than maxillary palps, stout, bearing minute very sparse setae. Trochanter extremely reduced, almost completely lacking laterally. Femur very short, annular, tibiotarsus at most slightly longer than broad, both very distinctly pigmented. Praetarsus stoutly conical, blunt, apical part sclerotized, seta absent.

Abdomen with broad poorly protuberant ambulatory ampullae (both dorsal and ventral) on segments 1 to 7. Dorsal ampullae divided by two laterally connected transverse lines, anterior one may be indistinctly doubled medially. Parascutum separated by relatively distinct curved impression from spiracular area. Spiracles similar to mesothoracic one, distinctly smaller. Epipleurum protuberant on segments 1 to 9, pleural tubercles or discs absent. Pleural lobes small, posterolateral, incompletely defined, coxal lobes separated from sternum by short deep impressions connected by two ± distinct transverse lines. Segments 9 and 10 small, caudal armature absent, anus triradiate, ventral radius very long, deeply cleaving ventral side of segment 10. Dorsal and ventral abdominal intersegmental zones not meeting precisely each other, but in details their arrangement differs from Cerambycidae. Large body areas (e.g. ambulatory ampullae, pterothoracic terga and sterna, hind half of pronotum, hind margin of prosternum, prothoracic coxal area and pleurum and other regions) very finely microspiculate.

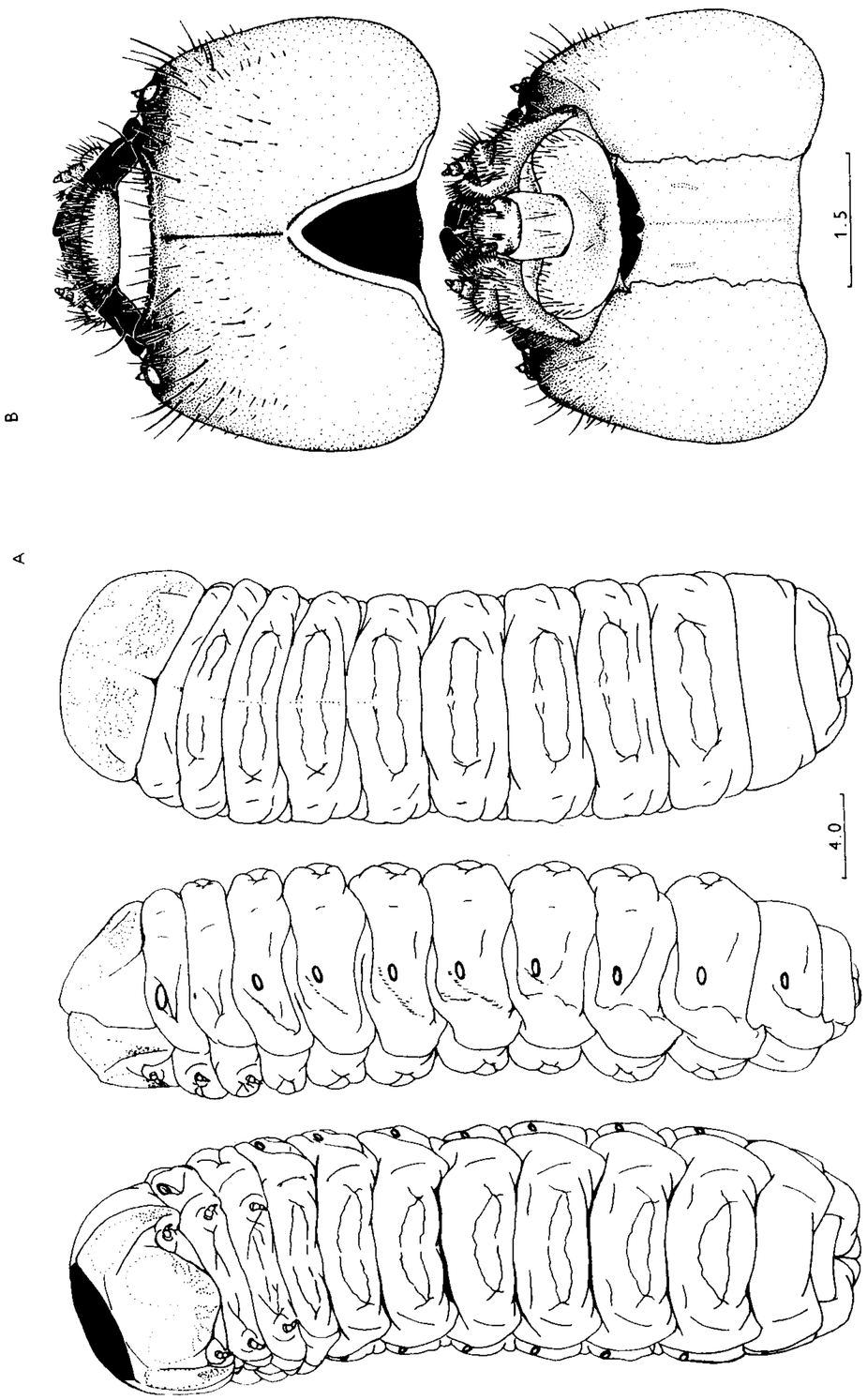


Plate 5: A — *Cheloderus childreni*, body (head removed), dorsal (right), lateral (middle) and ventral (left) views. (Setae not figured.) B — *Distenia gracilis*, mature, head, dorsal (upper) and ventral (lower) views.

Genus *Oxypeltus* BLANCHARD, 1851

Type species: *O. quadrispinosus* BLANCHARD, 1851 (monobasic)

Genus *Cheloderus* GRAY, 1832

Type species: *C. childreni* GRAY, 1832 (monobasic)

The two genera have altogether 3 species: *O. quadrispinosus, C. childreni* and *Cheloderus penai* KUSCHEL, 1955 (see CERDA, 1972). Larvae of *O. quadrispinosus* and *C. childreni* available:

1(2) Cranium deeply emarginate behind, nasale shorter, simple (Fig. 4B). Frons with transverse elevation low, less distinct. All six stemmata with very distinct pigment spots. Hypostoma flat, smooth. First segment of labial palp slender, much longer than broad. Single available larva 25 mm. . . . . *O. quadrispinosus*

2(1) Cranium very feebly emarginate behind, nasale more prominent (Fig. 4D). Frons with abruptly raised transverse elevation. Pigment spots small, not very conspicuous, that of ventral stemma nearly absent. Hypostoma somewhat protuberant, roughly rugose. First segment of labial palp only slightly longer than broad. Single available larva 39 mm. . . . . *C. childreni*

Oxypeltus quadrispinosus BLANCHARD, 1851

Host plant: Larva in *Nothofagus*, no other bionomical data available (DUFFY, 1960).

Distribution: Argentina, Chile (DUFFY, l. c.).

Material: 22. 5. 1954 Argentina, Patagonia, one larva from *Nothofagus dombeyi*, S. Schajovskoj lgt., coll. British Museum (the collector's name transcribed from the label).

Cheloderus childreni GRAY, 1832

Habits (CAMERON, REAL, 1974): Eggs laid on stems of living *Nothofagus*-trees, larva penetrates under bark and makes a J-shaped gallery about 10 cm deep in the wood oriented upwards. Fibrous frass expelled through the entrance hole or through other openings made in the bark. From the description it seems that the gallery in the wood serves for protection and the larva feeds mainly under bark where the gallery is broadened. The plant tries to heal the wound which causes callus visible on the stem. Pupation after about five-year larval life in the upper apical part of the gallery in the wood, the pupa turned head down. Pupae found from September to January, adults November to May. Egg stage apparently very long, several months. Larvae reach about 50 to 60 mm in length.

Distribution: Argentina, Chile, ?Colombia (doubtful according to CAMERON et REAL, 1974).

Material: IX. 1954 Chile, Llanquihue, one larva from *Nothofagus dombeyi*, G. Kuschel lgt., coll. British Museum.

Family Disteniidae LACORDAIRE, 1869

Larvae of single genus known and available.

Genus *Distenia* SERVILLE, 1825

Type species: *Distenia columbina* SERVILLE, 1825 (THOMSON design., 1860).

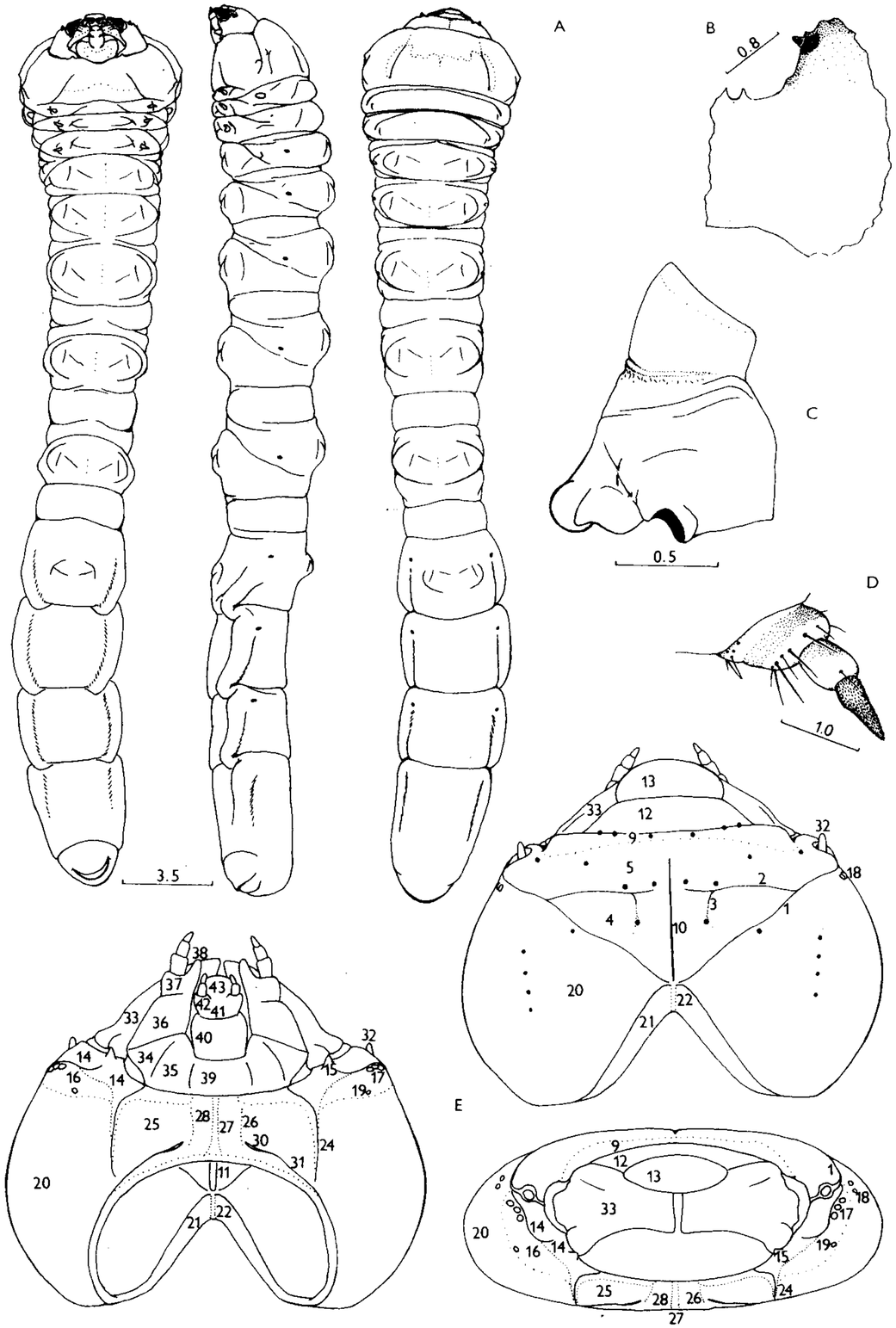
Body (Fig. 6A) white, extremely elongate, non-depressed except anteriorly where broadened, covered with moderately dense short setae.

Head (Fig. 5B) prognathous, about by half retracted. Cranium transverse (1.4–1.5), remarkably depressed (about 2.4), much narrower than prothorax, widest behind, mouthframe strongly sclerotized, hind half almost unsclerotized. Epicranium ± smooth, with sparse short anterior setae, dorsal row well developed, moved forward, epicranial sides roundly convex. Coronary suture ± absent, epicranial halves touching each other almost at one point at frontal base, dorsal cranial wall deeply notched behind. Frontal lines indiscernible except anteriorly where interrupting sclerotization of mouthframe below antennal opening; apparently they meet each other at anterior extremity of deep posterior cranial notch. Frons flat, finely anteriorly sclerotized, setal arrangement similar to Cerambycidae, transfrontal line and postcondylar carina absent. Epistomal margin strenghtened, sclerotized as in Cerambycidae, abruptly declivous, six main epistomal setae usually supplemented by several others. Distinct medial frontal line reaching epistomal margin. Clypeus almost unsclerotized, glabrous, trapezoidal, occupying entire space between dorsal mandibular articulations. Labrum strongly transverse, ± elliptical, basal half moderately sclerotized (strongly so at hind angles), anteriorly labrum broadly fringed with numerous stout setae, two discal setae not remarkably isolated. Epipharynx anteriorly with two paired groups of sparse setae, hind part moderately raised, with transverse row of rather long stout setae at anterior margin. Tormae rather long, curved backwards along sides of hind part. Pleurostoma moderately raised, sclerotized, subfossal process absent. Darker genal pigmentation up to about twice broader than pleurostoma. One large not very sharply defined moderately protuberant main stemma with fine pigment spot, other stemmata absent. Hypostomal lines and gula absent. Metatentorial bridge very broad, occupying almost all ventral medial cranial region, metatentorial pits non-developed.

Antennae short, three-segmented. Antennal ring sclerotized, esp. its medial part raised. Connecting membrane moderately large, allowing rather deep retraction of antenna. Segments cylindrical, sclerotized, second hardly as long as broad, third slender, usually longer than broad, main sensilla moderately large, abruptly prominent, elongate, conical. Mandibles corresponding with type I of Cerambycidae (Fig. 6C), moderately long. Apex and dorsal angle blunt, connected by simple cutting edge, outer face of apical part smooth, inner face with two ridges reaching apex and one very short at dorsal angle. Border zone moderately impressed, basal part bearing two lateral setae, molar region non-depressed, broad in medial view, esp. its dorsal margin distinctly carinate. Labiomaxillary complex moderately large, more retracted than in Cerambycidae. Connecting lobe sharply divided, anterior part smaller, hind part fused with submentum, whole area largely sclerotized. Cardo large, free, may bear minute seta. Stipes long, broad basal area sclerotized, inclosing ± distinct lateral pale spot (in *D. gracilis* sclerotization rather fine except for narrow strongly sclerotized basal band). Palpiger well defined, with broad ventral sclerotized area, palpiger process absent. Palp three-segmented, moderately long. Mala not borne from palpiger, short, stoutly cylindrical, densely setose, inner face not carinate, oblique pigmented band present. Mentum separated from submentum, with two transverse strongly sclerotized spots at hind angles, whole submentum gently sclerotized except for pale medial area. Labial palpigers defined, pigmented, palps slender, two-segmented. Ligula broad (palps separated by about 2 to 3 times their own width), rounded, bearing several ventral setae, apical face and lateral margins of dorsal labial part covered with very short dense microtrichia. Dorsal part very finely sclerotized, hypopharyngeal sclerome and hypopharyngeal bracon absent (in *D. gracilis,* but not in the other available undetermined American species, there is a small flat striated process at ventral mandibular articulation, pointed medially, normally covered with maxilla, suggesting vestiges of the latter bracon -- Fig. 6B).

Prothorax large, broadest of body segments. Lateral furrows distinct. Pronotum and alar lobes largely very finely sclerotized and pigmented, posterior half of pronotum and narrow adjacent regions of alar lobes finely distinctly microspiculate. Ventral margin of alar lobes with membraneous finely microspiculate tubercle, similar tubercle on upper margin of epipleurum just below and slightly behind that of alar lobe. Alar lobes posteriorly fused with epipleurum, latter fused ventrally with episternum and lateropraesternum, mediopraesternum delimited by shallow indistinct oblique impressions (perhaps secondary, similarly to most Cerambycidae Lamiinae), microspiculate posteriorly. Basisternum, sternellum and coxae fused into one transverse fold with two oblique impressions non-homologous with those separating coxosternum in Cerambycidae, latter fold microspiculate anteriorly. Epimeron ± defined. Anterior margin of praesternum behind labiomaxillary connecting lobes with a pair of tubercles similar to those on alar lobes and epipleurum. Prothoracic endoskeleton absent except for vestigial spina.

Pterothoracic nota microspiculate, particularly mesonotum with narrow separate anterior transverse area (I do not regard this area to be homologous with postnotum), otherwise mesonotum ± entire, metanotum with two lateral indistinct impressions on each side. Alar lobes only moderately protuberant. Epipleurum divided by deep oblique impressed line in two parts, posterior one rather poorly separate from pleurum. Mesothoracic spiracle not protruding into prothorax, moderately large, broadly oval, bearing several distinct marginal chambers along upper margin. Rudimentary metathoracic spiracle present but occasionally unpigmented and hardly visible. Praesternal triangle relatively large, not separated from anterior part of epipleurum. Small vestigial separate transverse area may be present between pro- and mesosternum, similarly to some Cerambycidae, e.g. many Lepturinae. Pleurum



broad, poorly defined dorsally, undivided. Coxae poorly incompletely delimited, transsternal line running from coxa obliquelly backwards, then indistinctly doubled and disappearing. Sternum and coxae largely microspiculate. Pterothoracic endoskeleton absent excepting rudimentary mesothoracic spina.

Legs (Fig. 6D) short, not much longer than maxillary palps, bearing sparse setae. Trochanter extremely reduced, almost absent in lateral view, with at most very few minute setae. Femur and tibiotarsus subequal in length, laterally finely sclerotized. Praetarsus very characteristic, unsclerotized, entirely microasperate, without seta.

Abdomen extremely slender and extended, anteriorly with distinct secondary segmentation (± complete intersegments present behind mesothoracic and anterior five abdominal segments, Fig. 6A). Abdominal terga moved remarkably forward in comparison with sterna like in Cerambycidae. Segments 1 to 6 bearing dorsal and ventral microspiculate ambulatory ampullae. Each dorsal ampulla with one lateral longitudinal and one discal oblique impressions on each side, ventral ampullae with rather similar pattern, pleural and coxal lobes not separated from each other. Lateral extremities of ampullae 2, 3 and less distinctly also 4 with more prominent tubercle. Epipleurum of segments 1 to 5 not protuberant, fused with spiracular area and whole region divided by deep oblique furrow. Epipleurum of segments 6 to 9 protuberant, that of segments 6 to 8 with inconspicuous pleural tubercle, pleural discs absent. Abdominal spiracles much smaller than mesothoracic one, broadly oval, posterodorsal margin with greater number of distinct marginal chambers. Ninth segment very long, up to almost twice longer than broad. Caudal armature absent. Anal segment reduced, posteroventral, almost fused with segment 9, anus transverse cleft (ventral radius rudimentary, ± absent).

Plate 6: A — *Distenia gracilis*, later instar larva, dorsal (right), lateral (middle) and ventral (left) views. (Setae not figured.) B — *D. gracilis*, later instar, part of ventral cranial wall (metatentorial bridge, hypostoma, ventral areas of pleurostoma and epicranium), ventral view. (Note flat short process behind ventral mandibular articulation, suggesting rudimentary hypopharyngeal bracon.) C — *D. gracilis*, later instar, left mandible, dorsolateral view. D — *D. gracilis*, later instar, left middle leg, anterior view. E — General scheme of Cerambycid head (Lepturine type), dorsal (upper right), anterior (lower right) and ventral (left) views. Generally, larger structures and areas are numbered mostly on the left half of each figure, smaller structures, lines etc. on the right half. (Numbering applies also to Plate 7, and some structures are not illustrated in the present figure.) 1 — frontal line, 2 — transfrontal line, 3 — blind pale postfrontal lines, 4 — postfrons, 5 — praefrons, 6 — postcondylar carina, 7 — frontal carina, 8 — epistoma (epistomal carina), 9 — epistomal margin, 10 — medial frontal line, 11 — endocarina, 12 — clypeus, 13 — labrum, 14 — pleurostoma (upper and lower part, perhaps only upper part should be called the pleurostoma), 15 — subfossal process, 16 — gena, 17 — main stemmata, 18 — dorsal stemmata, 19 — ventral stemma, 20 — epicranium, 21 — duplicated dorsal cranial region, 22 — medial cleavage line (perhaps at least partly homologous with coronary suture), 23 — inner cranial carina (made from inner layer of dorsal duplicated region), 24 — hypostomal line, 25 — hypostoma, 26 — gular line (raised lateral gular margin), 27 — medial gular line, 28 — gula, 29 — metatentorial bridge, 30 — metatentorial pits, 31 — postoccipital line, 32 — antenna, 33 — mandible, 34 — cardo, 35 — connecting lobe, 36 — stipes, 37 — maxillary palpiger with palp, 38 — mala, 39 — submentum, 40 — mentum, 41 to 43 — praelabium: 41 — praementum, 42 — labial palpiger with palp, 43 — ligula. Position of some main dorsal cranial setae indicated by dots: Six pairs of epistomal setae, four pairs of anterior frontal (= praefrontal) setae, one pair of postfrontal setae, one pair of adfrontal setae (originally situated on epicranium close to frontal lines), four miniature setae in a longitudinal row on each side of epicranium.

The genus is distributed in America, Eurasia and Africa, most species found in Central and South America. One single species in the region dealt with.

Distenia gracilis BLESSING, 1872

Habits: Polyphagous on deciduous trees. Larvae feed under bark and in dead wood, pupation in early summer in the wood, emergence in summer. Two-year life cycle according to CHEREPANOV 1979).

MAMAEV and DANILEVSKY (1975, p. 19, confirmed personally by my co-author) draw attention to the fact that habits of the mainland population differ from those of the population on the Kurile Islands (and consequently maybe also in Japan). In the Ussuri region the larvae feed under bark and in rotting wood at or under ground level, mostly pronouncedly in roots, while the Kunashir population has been found to inhabit dead fallen stems. Similar differences are mentioned by CHEREPANOV (1979). It is possible that we are facing two separate taxa. However, reliable larval morphological differences have not been found.

Distribution: Ussuri region, N-E China, Korea, Sakhalin, South Kurile Islands, Japan.

Material: 1972 - 77 SU, Kurile Islands, Kunashir, 12/I, *Alnus, Betula. Ulmus,* lgt. A. V. Kompantsev, S. Korolev and D, coll. IS and S; 1967 - 74 SU, Ussuri region, Kedrovaya Pad' Nature Reserve, 9/I, *Chosenia*, lgt. D, coll. IS.

In addition to the above material of *D. gracilis*, the generic description is based on two larvae of an indetermined American species (14. 10. 1941 Mexico, under bark of mahogany log, coll. U. S. Natn. Museum Washington) which appeared in all important characters similar to *D. gracilis*. There is one interesting difference, namely the absence of the process figured in 6B.

Existing descriptions of a few other species (Indian *D. dravidiana* GAHAN, 1906 by GARDNER, 1931a; American *D. undata* (F., 1775) and *D. rugiscapis* BATES, 1885 by CRAIGHEAD, 1923) suggest they are very similar, too. According to CRAIGHEAD (l.c.), the larvae of *D. undata*, and perhaps also *D. rugiscapis*, possess small maxillary palpiger process.

Family Cerambycidae LATREILLE, 1804

General morphology

Note: Although in fact they do not belong there, I have also included some functional or other remarks in the general morphological chapter, believing they would be more convenient and easily understandable next to the appropriate morphological data.

Larvae eucephalic, oligopodous to apodous, ± elongate, cylindrical to strongly depressed. Body white, yellowish, rarely greyish, generally unsclerotized (except

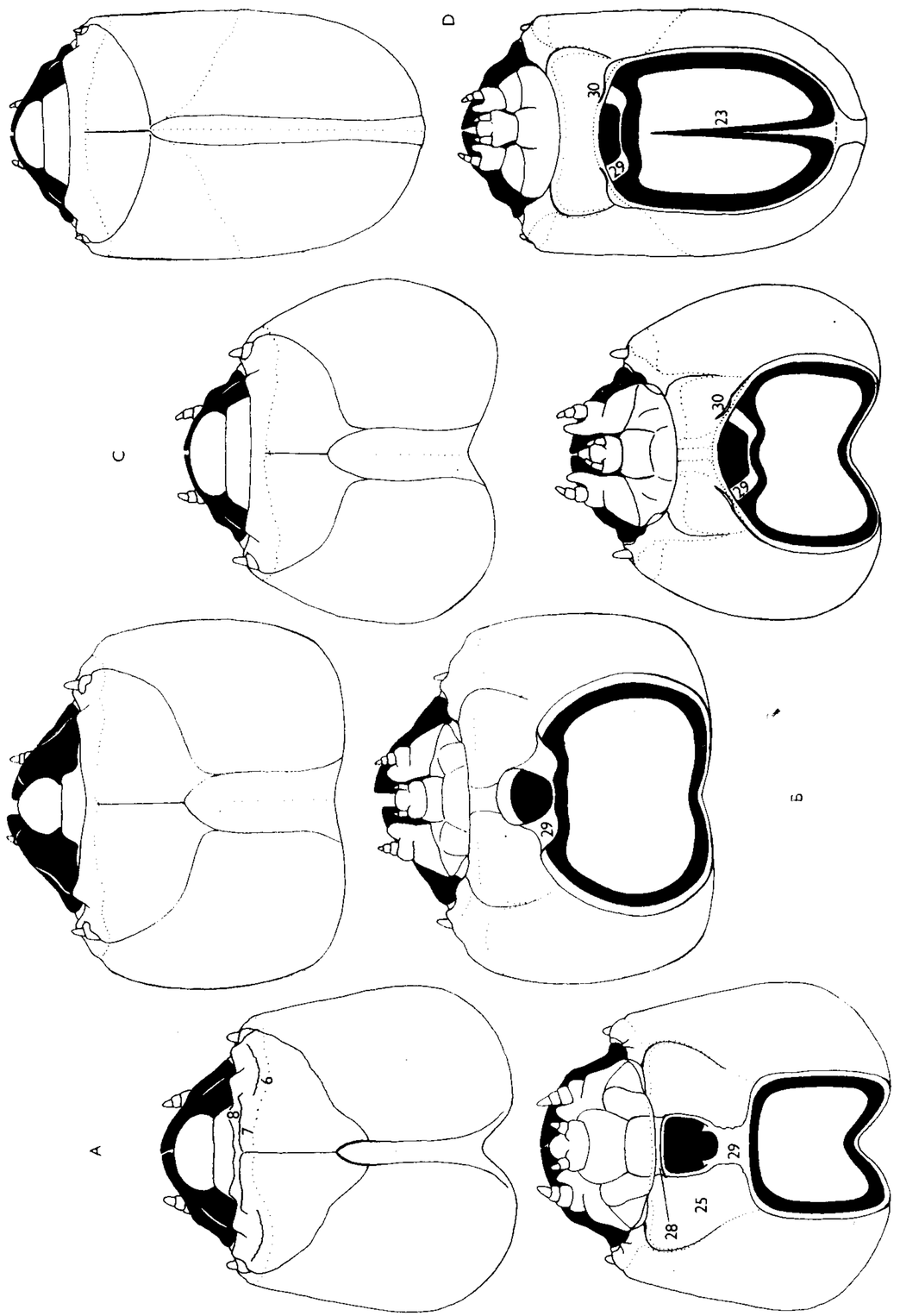


Plate 7: Head types of some Cerambycid subfamilies, dorsal (upper) and ventral (lower) views. A — Prioninae, B — Cerambycinae, C — Aseminae, D — Lamiinae. (For explanation of numbers see Plate 6.)

for some areas of prothorax, spiracles, caudal armature of some species and some special sclerotized structures serving for support in galleries, e.g. areas covered with microscopical cuticular spines - other sclerotizations rarely occur). Abdomen with at least dorsal ± protuberant retractile locomotory structures, the so-called ambulatory ampullae.

Head (Figs 6E, 7A-D) prognathous due to sclerotized ventral region (the gula - - commentary see below) and retraction of the dorsal portion into prothorax.

Cranium slightly to very strongly depressed dorsoventrally, at least partly retracted into prothorax (only slightly in some Lepturinae and some Lamiinae), ± longer than wide in Lamiinae, subquadrate to distinctly transverse in other subfamilies.

Frons and frontal lines: It is possible (or even probable) that in some Coleoptera larvae (incl. Cerambycidae) the »frontal sutures« are, at least in their middle section, secondary cleavage lines, non-homologous with frontal sutures of other insects. A neutral term »frontal lines« is therefore used (the term »frons« has been preserved regardless of its possible other meaning). A possible way how these lines might originate from the type with deeply incurved frontal sutures (which can be seen e.g. in some Cucujoidea) is given in Fig. 8C. Indistinct diffuse incurved portions of the original frontal sutures are still discernible in some species of various subfamilies. The shape of the incurved frontal sutures caused by dorsal tentorial arms (resting on epicranium close to the latter sutures) being pushed mesad, perhaps by increasing mandibular muscles. Apparently these arms are uncapable of crossing functional frontal sutures, since the peculiar incurved shape has no obvious advantage, in fact it should be disadvantageous during ecdyses. In Cerambycidae, the dorsal tentorial arms are very much reduced, yet (in the few species studied) more or less reaching dorsal cranial wall in the frontal region on both sides of endocarina (see below), i.e. exactly in the spots expected by the above »frontal-line« concept. Moreover, the antennal retractor muscles (attached originally on the tentorium, but in many coleopterous larvae attached on dorsal cranial wall in epicranial region due to reduction of the intracranial tentorial structures) are in Cerambycidae attached on frontal region, namely on anterior postfrontal angles (when the transfrontal line developed), which is also in full concordance with the above concept. Lateral sections of the transfrontal line (see below) and longitudinal pale lines in postfrontal region of some Lepturinae (Fig. 6E) may well represent modified remains of the original frontal sutures, too. Frons triangular to half-circular or half-oval. Frontal lines in species with pigmented cranium mostly as ± sharp pale lines, rarely cuticle along them unpigmented; often quite indistinct when the whole cranium unpigmented. Anteriorly frontal lines either bisect antennal ring and enter antennal opening (mostly passing through to the anterior cranial margin), or only touch this opening from below, or end blindly near it.

Transfrontal line (transverse cleavage line) developed only in many Lepturinae (in varying degrees, always absent from very young larvae). Frons in such case divided

into anterior (praefrons) and posterior (postfrons) regions. Frons strengthened medially by internal apodeme (the so-called endocarina), usually externally manifested as a darker medial frontal line; it may or may not reach the anterior (epistomal - see below) frontal margin. In some Lepturinae pigmentation is less pronounced in the region of transfrontal line. Very rarely endocarina absent. In most Prioninae, a curved postcondylar carina developed on each side behind the dorsal mandibular articulation; vestigial postcondylar carinae may also be found in a few Cerambycinae.

Anterior margin of frons always strengthened, infolded (Fig. 8A), ± strongly sclerotized, probably of complex origin. As the secondary (dorsal) mandibular articulation (originally situated probably on the base of clypeus) is placed on the anterior frontal margin, because the epistomal setae (see below) are with greatest probability homologous with the clypeal setae of other families, and finally because in other families can be found clear transitional situations, it seems very probable that the anterior margin of frons incorporates the basal part of the clypeus, i.e. the postclypeus. This is probably why CRAIGHEAD (1915, 1923) named this margin epistomal, or epistoma (in most Prioninae, *Apatophysis* and a few Cerambycinae, a separate transverse ridge or keel is developed between the frons and the clypeus proper, or anteclypeus; it is then simply called the epistoma, although it is not clear as to whether or not it represents the incompletely joined postclypeus - at least in some cases it might well be a secondary structure, e.g. for support in galleries). In many Prioninae the epistoma, as well as the following frontal margin, are dentate and/or carinate, mainly in later instar larvae. The epistoma or epistomal margin bear so-called epistomal setae (originally probably postclypeal), usually four in Cerambycinae, six or more (with very rare exceptions, e.g. some *Prionus*-species) in other subfamilies. In the Cerambycinae, however, the medial pair of epistomal setae was not probably lost but pushed backwards, becoming the anterior medial pair of frontal setae. Very rarely (some Methiini, fig. 13E) the four epistomal setae of Cerambycinae are multiplied. Anterior frontal angles form the dorsal portion of the antennal ring (often raised and strongly sclerotized), or - when frontal lines do not enter antennal opening - wholly surround the antennal base.

Clypeus (in fact probably anteclypeus, see above) slightly convex to flat, mostly ± trapezoidal, only in Cerambycinae abruptly narrowed from the very base, so that the whole anterior portion (by far greatest; at first sight the whole clypeus) does not fill the space between dorsal mandibular articulations. Clypeus mostly devoid of setae, only in some Lepturinae and Lamiinae regularly with a few lateral macroscopic thin-walled setae*), mostly of inconstant number. Lateral seta may also occur

*) Note: The term »seta« is used in its broadest sense, including all bristle- or hair-like ± articulated sensilla, i.e. also certain bristle-like chemoreceptors. Sharp distinction is, however, made between setae and microtrichia, i.e. non-articulated cuticular outgrowths not formed by the specialized cellular complex typical for all sensilla. Microtrichia are usually very fine, and almost never occur singly. Usually they may be distinguished without difficulty, but if doubts arise, a microscopic slide will always help - microtrichia are neither hollow nor innervated (Fig. 13A).

in some individuals of other species. In most species there are only a few lateral non-projecting sensilla (it seems that the setae originated from some of these sensilla by re-acquiring trichoid form, as none of the groups with regular clypeal setae can be considered primitive). Basal and/or lateral regions of the clypeus may be sclerotized and pigmented.

Labrum of variable size and shape, rather small in Cerambycinae; from rather long (e.g. *Parandra,* Fig. 14E) to strongly transverse (long cordate labrum usually corresponding with mandibular type II - see below - covering the dorsal striated plates), from distinctly convex to flat. Anterior margin bearing setae, two or more discal setae present, occasinally the whole anterior half setose and the discal setae indistinguishable from others. Labrum may be dorsally sclerotized to varying extent, apex always membraneous. Epipharynx with its anterior region (corresponding with the labrum) flat, mostly with ± numerous setae, often with microtrichia. Hind epipharyngeal region medially ± longitudinally raised (very abruptly e.g. in *Parandra,* Fig. 14D, or some Prioninae, Fig. 19C), mostly with microtrichia along sides, always with some sunken sensilla behind (often with two paired groups of five distinct sensilla, e.g. Figs 27D, F). Setae may reach far behind along hind raised portion (Fig. 19C). The tormae (i.e. two paired transverse or backwards curved sclerotized bands ± continuous with the basal dorsal sclerotization of the labrum) always present, but sometimes very short and reduced. A sclerotized longitudinal band may be present running along sides of the hind portion, occasionally connected with the torma of its side, making it very long. In some species, each torma may have an anterior or anteromedial branch (very long in *Nothorhina,* Fig. 28E, making the tormae T-shaped). Approximately between the bases of tormae, a medial group can always be found of variously shaped setae and/or other sensilla, frequently arranged in a transverse row (Figs 27D, F), may link the longitudinal rows of setae (Fig. 17B). The hind raised portion in some species with a ± distinct sclerite.

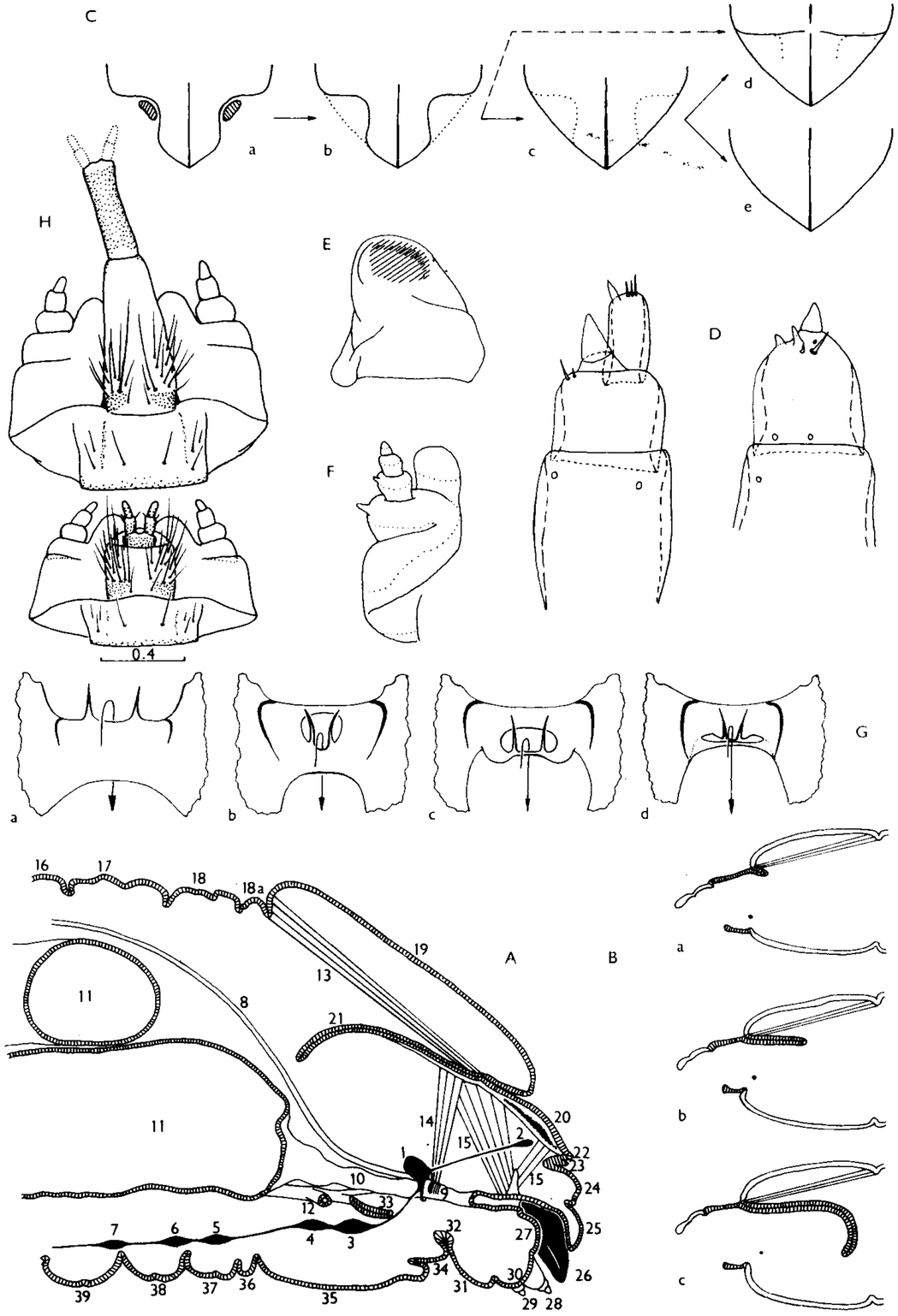
Lateral part of anterior cranial margin (between frontal and hypostomal lines), mostly strengthened and markedly sclerotized, has been called the pleurostoma by CRAGHEAD (1915, 1923). Other authors have used other terms for this region (and for CRAIGHEAD's gena as well, see below). The pleurostoma (sensu CRAIGHEAD) apparently of a complex structure, not homogeneous, usually ± distinctly divided into upper and lower parts (Fig. 6E); almost always devoid of setae, may be variously sculptured. The lower part with a pit (»fossa mandibularis« - cf. subfossal process, see below) for the primary, or ventral mandibular articulation. Next to it, pleurostoma often projecting into a ± prominent tubercle or process, called the subfossal process owing to its position. (In fact only the upper part should be probably called the pleurostoma, the lower part with the mandibular articulation rather elaborate because of mechanical demands, perhaps incorporating basal parts of hypostomal ledges, and hard to interpret as belonging to a certain cranial region.)

The remaining area of the lateral part of cranium is called the epicranium, or two epicranial halves. One epicranial half is delimited by the posterior margin of

pleurostoma, frontal line, coronary suture, margin of occipital foramen and hypostomal line. The anterior region of epicranium immediately behind pleurostoma often distinguished from the remaining surface by sculpture and/or coloration. This area, the gena (sensu CRAIGHEAD), has no constant topographic range, the latter greatly varying in various species.

The rest, the epicranium proper, constitutes the largest cranial area and serves for attachment of all mandibular muscles. The anterior epicranial region (incl. gena) always bearing setae, hind region (retracted or retractable into prothorax) glabrous except for ± longitudinal row of miniature setae (mostly four on each side) usually present on dorsal surface, perhaps informing about the position of head to prothorax.

Right and left epicranial halves meet dorsally at the base of frons. Exposed coronary suture non-developed, dorsal head retractors attached just behind the point of contact of both frontal lines or even somewhat before it (at the frontal base, then the frontal lines enter separately the dorsal doubled cranial region - see below and Figs 7A, B, C). However, with the exception of Necydalinae and most Lepturinae, the epicranium is broadly fused behind this attachment, i.e. internally. Cranium thus formed seems to have dorsal retractors attached not to the edge of occipital foramen (although not the present cranial margin, but the line along which prothorax is attached to cranium should be probably regarded as the original hind cranial margin). Therefore the internal portion of the cranium behind the attachment of the dorsal retractors must be (and is) double-walled (both layers can be sometimes separated, e.g. after boiling in hydroxide). It is not clear whether the dorsal layer of the doubled region is of cranial or »postcranial« origin, but the former alternative seems to be more probable. In Necydalinae and most Lepturinae the doubled region is only short (Fig. 6E), or the epicranial halves meet in »one point« only. A diagram of »narrowly« and »broadly« fused epicranial halves is given in Fig. 8B, to be compared with Figs 6E, 7A to D. The epicranial halves are completely fused in Lamiinae, where they are jointly rounded posteriorly and head form resembles in dorsal view e.g. that of Bostrychid larvae, although its evolution and construction are quite different from Bostrychidae. The advantage of such construction probably lies in the possibility of attaching muscles to dorsal head surface while mandibular muscles in the hind part of cranium get enough support necessary for work in hard material. (In Bostrychidae and similar larvae with normally constructed heads, working in hard material, the »disadvantage« due to the impossibility of attaching muscles to dorsal head surface and the consequent inability to move the head upwards by force has been probably compensated by C-shaped body and rotation of larva in gallery.) In some Lamiinae with a deeply retracted head the cuticle of the posterior region of the epicranium is cemented to the inner surface of the prothoracic »pocket« in which it is retracted (Fig. 7D, the region behind the transverse dotted line on epicranium). In the middle of the duplicated region lies the line along which breaks the cephalic cuticle during eceysis and which probably corresponds with the coronary suture of



a normal head. Often (particularly in Lamiinae) the ventral layer of the duplicated region is medially longitudinally folded inwards, forming a crist ± deep inside the cranial cavity, continuous with the endocarina.

The ventral cranial wall laterally delimited by two dark lines called hypostomal, which externally manifest two internal sclerotized ridges beginning in the strengthened anterior cranial margin a little below the ventral mandibular articulation. In some Lamiinae the hypostomal lines are vestigial. The ventral cranial wall consists of two hypostomal plates (or hypostoma) medially bridged by the gula (or gular area if the border lines are indistinct). Gula apparently originally with raised lateral margins suggesting the original free space between the hypostomal plates having been covered by a secondarily sclerotized layer. CRAIGHEAD (1923), commenting upon the absence of gula in the genus *Distenia* (see family Disteniidae in the present paper) writes about the origin of the gula (p. 16): »*Distenia* is also peculiar in that, apparently, no gula is present, the submentum articulating directly by the collar to the prothorax. The writer believes, however, that this portion of the collar in reality is the gula, or rather that it has been termed the gula when it has become chitinised

Plate 8: A — Diagrammatic submedial section through anterior part of a Prionine larva (drawn essentially from *Megopis*), with arrangement of some internal organs. Cuts are hatched. 1 — cerebral ganglion, 2 — frontal ganglion, 3 — suboesophagial g., 4 — prothoracic g., 5 — mesothoracic g., 6 — metathoracic g., 7 — first abdominal g., 8 — dorsal vessel, 9 — pharynx, 10 — oesophagus (9 + 10 — stomodaeum), 11 — mesenteron, 12 — large tracheal cross-connection between left and right tracheal systems, 13 — main dorsal head retractor, 14 — main dorsal pharyngeal muscle, 15 — muscles attached to lateral sclerotized plate-like broadening at mouth opening, 16 — first abdominal tergum, 17 — metanotum, 18 — mesonotum (18a — postnotum), 19 — pronotum, 20 — frons, with endocarina, 21 — dorsal duplicated cranial region, 22 — frontal carina, 23 — epistoma (epistomal carina), 24 — clypeus, 25 — labrum, 26 — mandible, 27 — hypopharyngeal portion of labium, 28 — maxilla, 29 — labial palp, 30 — ligula, 31 — mentum and submentum (postlabium), 32 — gula (in this species fully concealed by 34), 33 — metatentorial bridge, 34 — postgular lobe, 35 — prothoracic praesternum, 36 — sternellar fold, 37 — mesosternum, 38 — metasternum, 39 — first abdominal sternum. B — Diagrammatic medial sections of prothorax, cranium incl. tentorial bridge (hatched), clypeus and labrum (with position of main dorsal head retractor muscles), showing short (a, e.g. most Lepturinae), long (b, e.g. Aseminae) and very long (c, only Lamiinae) dorsal duplicated cranial region (compare with fig. 6E and Plate 7). C — Probable origin of present frontal lines from the situation with frontal sutures deeply incurved (a) due to the dorsal tentorial arms (resting on the epicranium - hatched areas) being moved anteromedially, perhaps due to increasing mandibular muscles. Situations (a) and (b) do not occur in Cerambycidae, situation (c) can be found in very few species (e.g. certain Lepturinae), but the original incurved sections of the frontal sutures are always diffuse and ± indistinct; (d) found in many Lepturinae (the distinct transfrontal line is, in my opinion, a secondary structure, and has been preceded by (c), not by (b)); situation (e) occurs in most Cerambycidae. D — Three--segmented (left) and two-segmented (right, third segment lost) Cerambycid antennae (from DUFFY, 1953). E — Typical shape of mandible of Cerambycinae (right mandible, medial view). F — Outline of maxilla of Cerambycinae with processes on palpiger and first palpal segment, lateroventral view. G — Diagrammatic illustrations of various types of construction of ventral cranial wall (ventral regions of pleurostoma and epicranium, hypostoma, tentorial bridge with dorsal arms, and gula, if present) in dorsal view, i.e. as if viewed from the cranial cavity. The arrow indicates the nerve cord (leaving the cranial cavity always before the tentorial bridge - cf. fig. A). Situation (a) showing absence of gula, metatentorial bridge hypertrophied (families Vesperidae through Disteniidae), (b) found in Prioninae and Parandrinae (cf. figs 7A, 14C), (c) found in Cerambycinae, *Apatophysis* and nearly so in some Aseminae (cf. fig. 7B), (d) found typically in Lepturinae (cf. fig. 6E). H — *Pseudobottegia* sp. (Cerambycinae, Africa), labiomaxillary complex (maxillae in outline), showing telescopic praelabium in protracted (upper) and retracted (lower) positions.

and is attached to the surface of the fused hypostomal plates or lies between these plates when they are separated.« The present author fully agrees with the main concept of the cited text, i.e. that the surface layer of the gula is not of cranial origin but represents the sclerotized connecting membrane between labium and prothorax (maybe with some part of labium incorporated). In Prioninae and Parandrinae, gula is very short, strongly transverse, often almost invisible externally, being covered by a separate lobe (here called the postgular lobe, Fig. 8A, present in Prioninae, Parandrinae, usually small in Cerambycinae, usually ± absent in other subfamilies where, however, certain posterior gular areas might possibly have originated from the postgular lobe), in other subfamilies gula mostly longer, exposed and visible externally (or at least can be exposed simply by pushing back the anterior margin of prothorax - this concerns mainly badly fixed contracted larvae, where head is often retracted very deeply in prothorax). Very short gula (perhaps secondarily covered by the expanded submentum, also the postgular lobe is relatively large) can also be found in the Cerambycine tribe Methiini (see chapter on problematic larval forms). Raised lateral gular margins are called the gular lines in the present paper; they are often obliterated. Gula moreover often with a medial brightening (apparently corresponding with the medial gap between hypostomal plates), occasionally transformed into a ± distinct pale medial gular line. Gula and hypostoma form together quite a distinct unit, particularly in Aseminae, Necydalinae, Lepturinae and Lamiinae, where the gular lines may be completely absent, and the whole region is then collectively called the ventral sclerite.

Metatentorium built differently in various subfamilies. In Prioninae and Parandrinae it forms a wide rigid sclerotized bridge in the plane of hypostoma, thus apparently dividing the occipital foramen into two parts; metatentorines (metatentorial pits) are absent as the metatentorial arms are invaginated from the border between cranium and the postcranial membraneous region (Fig. 7A, 8A). In other subfamilies, the middle section of the metatentorial bridge is very narrow, ligamentous or only weakly sclerotized. In Cerambycinae and *Apatophysis* at least the proximal parts of the metatentorial arms lie in the plane of hypostoma, and the occipital foramen seems to be divided in the ventral view, distinct metatentorial pits absent with rare exceptions (Fig. 7B). In other subfamilies metatentorium extends ± obliquely inside the cranial cavity (however, some Aseminae are close to the Cerambycinae situation, Fig. 25D, E). In Lepturinae and some Aseminae the metatentorium is fully internal, invisible in ventral view, and the occipital foramen does not seem to be divided. In Lepturinae, Necydalinae, Aseminae, Lamiinae and *Dorcasomus,* a narrow region behind the metatentorial invaginations sclerotized so that the spots of invagination become distinct as narrow slits - the metatentorial pits, or metatentorines, (The situation may be also interpreted as that the metatentorial arms have moved anteriorly, thus occurring fully in the sclerotized cranial region, but the former interpretation seems more correct.) The metatentorines are, however, rather indistinct in some Aseminae, and, on the other hand, they are ± developed in a few Cerambycinae, e.g. in the Australasian genus *Blosyropus*; the genus *Apatophysis* also tends to develop metatentorial pits.

The metatentorial bridge is a very important limit inside the cranial cavity. As long as it exists, it cannot be crossed by internal organs, so with changes of its position must take place changes in their arrangement and vice versa. E.g. nerve cord always leaves the cranial cavity through the metatentorial arch, i.e. through the anterior part of »divided« occipital foramen (Fig. 8G), digestive tube always outside (above) this bridge, i.e. through the posterior opening. I never have seen any species with the transverse metatentorial bridge fully reduced (the figure of *Phymatodes albicinctus* by KOJIMA and HAYASHI, 1969, Fig. 11/2, showing complete absence of metatentorium, is incorrect - personal observation). However, as the bridge is extremely fine and slender in some species (particularly in Lamiinae where usually torn off during dissection), it cannot be excluded that there may be some Cerambycidae with the left and right metatentorial arms disconnected.

Dorsal metatentorial arms (in the very few species studied) extremely reduced, leading inside cranial cavity towards frontal region. Protentorium extremely reduced, too, protentorial pits indiscernible from outer view (they are distinct in the Oxypeltidae), protentorial arms originate between dorsal mandibular articulations and antennae, and are vestigial, short, very slender, pointed ± backwards. As far as I have been able to ascertain, the pro- and metatentorium are not connected with each other. The remarkable reduction of the tentorial structures, except for the metatentorial bridge of some groups, should be perhaps ascribed to the enormously developed mandibular muscles filling most of the cranial cavity. The tentorial structure also shows that the dorsal tentorial arms (the supratentorium of some authors) belong to posterior tentorial arms, not to the anterior ones as mostly supposed, since in the disconnected pro- and metatentorium the dorsal arms remain connected with the latter. Calling the spots of attachment of the dorsal arms to dorsal cranial wall »supratentorines« (e.g. BITSCH, 1966) seems to me incorrect and misleading; unlike the pro- and metatentorines, they are not points of invagination, the dorsal tentorial arms only resting from the inner side on the cranial wall.

Antennae rather short to miniature, relatively longest in some Cerambycinae, originally three-segmented, third segment may be totally lacking, the second may be very much reduced, so that antennae may be ± one-segmented (e.g. the Lepturine genus *Dinoptera*). In some Lamiinae, on the other hand, ± fuse segments 1 and 2. Antenna joined to cranium by membrane, called here connecting membrane; other authors mostly call it basal membrane which seems confusing to me (cf. the basal membrane on the underside of insect epidermis). Connecting membrane usually largely attached to the first antennal segment, so that only apical part of the latter is free. Membrane ± extended outwards, antenna therefore ± retractile. First two segments mostly cylindrical, the second annular in its reduced states. Third segment, if present, placed excentrically on the apical face of the second segment, together with a few small sensilla and one large (in comparison with others), although not necessarily

longest compound sensillum (cf. SCOTT et ZACHARUK, 1971). The latter sensillum (in descriptions usually referred to as the main antennal sensillum) flat (rarely roundly convex, Figs 15D, 20D) in Prioninae and Parandrinae, conical (sometimes rather minute) in all other subfamilies (e.g. Figs. 30 E, F). Apical sensilla of the third and/or second segments do not disappear with their reduction, being preserved on the apical face of the second (first) segment. Antennal base mostly surrounded by a raised sclerotized antennal ring, rarely the connecting membrane passing smoothly into the cranial wall.

Stemmata occur at most in six pairs, may be entirely lacking (for the possible occurrence of the seventh stemma see general morphology of the Parandrinae and Prioninae, cf. Fig. 18B). Situated in the genal area, distributed into three groups. The first group, originally consisting of three stemmata, placed on the border of pleurostoma and gena just below the antenna, and called the main stemmata in the present paper. All stages of fusing and reduction occur. The second group, the dorsal stemmata (originally two), can be found a little behind and above the main ones. Mostly less distinct; all degrees of fusing or reduction. The last ventral stemma lies behind and below the main stemmata. Often without pigment, or absent. (Attention! The pigment of preserved larvae may be torn off and become invisible in outer view.)

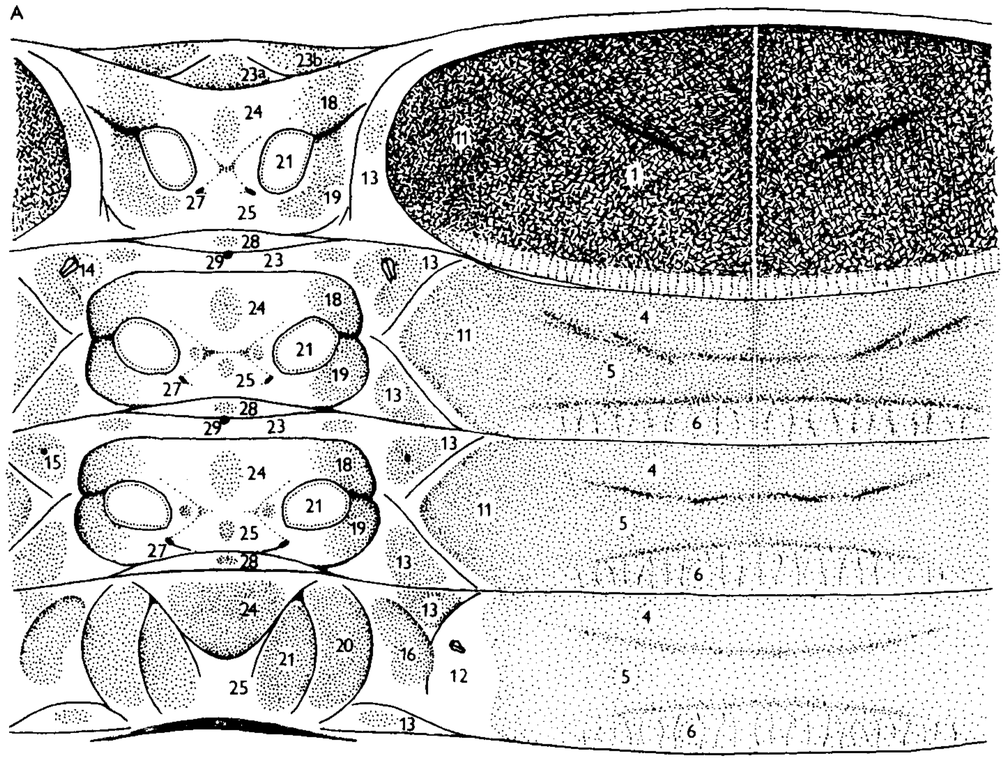
Mandibles are one of the individually most variable structures, although in varying degrees in various groups. Moreover, they may be subject to extensive abrasion during each instar, so that their sculpture may become ± lost. Always strongly sclerotized due to the way of life. Ventral articulation by condylus to pleurostoma, dorsal by ginglymus to the epistomal margin of frons. Two apodemes are developed at the base of the mandible, protruding deep inside the cranial cavity; the slender lateral one for a weak mandibular abductor, and the medial one, large and complex, for attachment of a very large and strong mandibular adductor. The mandible is variously shaped, mostly ± distinctly divided by a slight transverse depression into basal and apical parts. Basal part without any special molar structures or articulated appendages, in later instars often variously sculptured; with at least two lateral setae, often with more, in some Prioninae with a group of ± numerous short setae on dorsomedial face (e.g. Fig. 17D). Apical portion highly specialized in Cerambycinae (Fig. 8E) where it is rounded, spoon-like (or the term "gouge-like" has been used in literature), with a smooth inner face. In other subfamilies the apical portion with ± produced apex and so-called dorsal angle. Two basical types of the apical part may be found, with all intermediate situations. One of these types (in descriptions referred to as the mandibular type I) characterized by the apex and dorsal angle connected by a simple cutting edge, usually emarginate or slightly angulate, the dorsal face of the apical part ± simple, smooth (e.g. Fig. 26D). Inner face with two or three ± distinct keels or ridges running towards apex (they may be abraded and almost absent). The second type (type II in descriptions), more complex but perhaps more ancient, with two or three inner ridges at apex as in the type I.

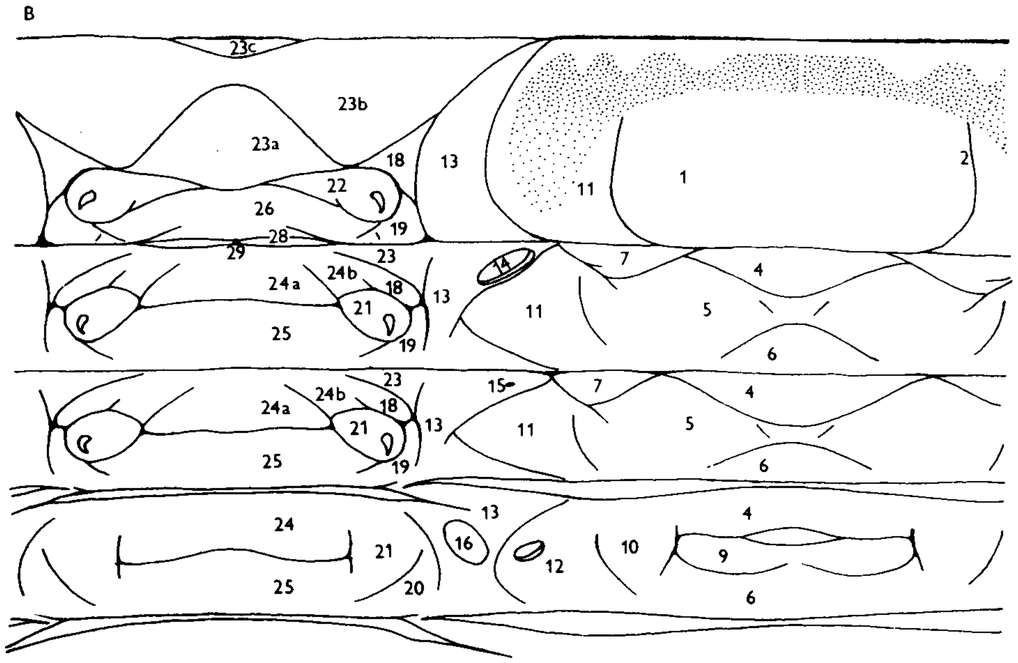
Cutting edge reduced, pushed laterad, usually forming a ± distinct angulate costa on the dorsal face of the apical part. However, another strong keel developed, beginning at dorsal angle, may or may not reach apex. Dorsal and inner face of this keel very often striate or otherwise remarkably sculptured (Figs 17D, 23A, 30C). Both types with all transitional situations may be found in the Lepturinae, Necydalinae (Figs 24G, H, I) and Aseminae, type I in the Lamiinae, type II (occasionally strongly modified and resembling type I, e.g. in *Prionus*) in the Prioninae and Parandrinae. *Apatophysis* has the type I, the genus *Dorcasomus* with small type II - keel present. Mandibular apex sometimes double (e.g. Fig. 13C, also in some Lepturinae and Lamiinae). The apical mandibular part always devoid of setae.

Maxillae and labium fused by their basal parts, forming the labiomaxillary complex. Base fused almost without traces in Lamiinae, where it is firmly attached along the whole its width to the anterior cranial margin (Fig. 7D). In other subfamilies the base ± distinctly superficially divided into an unpaired medial submentum, paired intermediary connecting lobes of uncertain origin, and cardines. Cardo free in these subfamilies, ± movable (i.e. not immovably attached to the anterior cranial margin), only in some Aseminae cardo very much reduced making the situation close to that of Lamiinae. Cardo usually sclerotized, but never with two distinct separate sclerites. The connecting lobes are usually not divided into two parts, or the anterior part is much smaller than the posterior one.

The free distal maxilla consists of stipes, maxillary palpiger, mala and maxillary palp. Maxillary palpiger rather distinctly separate from stipes, the palp three-segmented, rarely two-segmented (fusing of segments 2 and 3). Palpiger in most Cerambycinae, Apatophyseinae, some Aseminae and a few Prioninae with a ± prominent laterodorsal process (e.g. Figs 17E, 26E), in some Cerambycinae the first palpal joint with similar process (Fig. 8F). Mala of various shapes from large triangular to slender and finger-like, always bearing stout setae. No traces of border line between galea and lacinia. When narrow and finger-like, the mala in ventral view mostly makes the impression that it grows out exclusively from palpiger (all Lamiinae and Aseminae - Fig. 29H, most Lepturinae, certain groups of other subfamilies), but in dorsal view the line separating mala and palpiger always remains visible.

Free distal labium consists of mentum and praelabium (praementum with labial palpigers, labial palps and ligula). Dorsal (inner) portion of labium is of hypopharyngeal origin (salivarium absent). Mentum sometimes ± not separated from submentum. Labial palpigers less distinctly separated from praementum, labial palps two-segmented. Ultimate segments of both maxillary and labial palps with apical or subapical sensory area. Ligula simple, undivided, ± membraneous. Hypopharyngeal portion at most with weak sclerotizations, never with the hypopharyngeal sclerome (see BÖVING and CRAIGHEAD, 1931). Sclerotized bridge between cranium and labium (the hypopharyngeal bracon, l. c.) absent. Free labium curiously modified in *Pseudobottegia* sp. (Cerambycinae) where the praelabium is elongate, deeply retracted in mentum, may be protruded far forward (Fig. 8H).





Various regions of labiomaxillary complex may be sclerotized and pigmented. All its parts may and mostly do bear setae, esp. the ligula, moreover, often with distinct microtrichial cover. In descriptions, the labiomaxillary complex is described mostly from ventral view only.

Thorax and abdomen (Figs 9A to 12A): As to the morphological terminology of the thoracic and abdominal areas, a few changes have been made in comparison with the terminology of CRAIGHEAD (1916, 1923), which has been mostly used since the years of publishing. Changes concern chiefly thorax and are based on comparative study, study of the muscles etc. The terminology used can be better understood when compared with the situation in some sclerotized coleopterous larva with the individual areas clearly defined. In the Fig. 9A I therefore give a diagram of the thoracic and abdominal areas of the *Byrrhus*-larva (Byrrhidae) where the tergum is ± entire indeed, but the pleural and sternal regions which have been main subject of changes are well developed.

Meso- and metathorax are of very similar structures and they will be described first, as they exhibit the most generalized situation.

Meso- and metanotum each often divided by two transverse curved lines into anterior praescutum, posterior scutellum, and the scutum between them. Both lines are medially brought together, narrowing the middle of the scutum, or even fused at middle into an X-shaped pattern. In many derived forms all these lines may be reduced up to an entire undivided notum, or modified - e.g. only one ± straight transverse line which is ± homologous with the anterior line separating off the praescutum (this situation can be found in metathorax of many Lamiinae or Cerambycinae). Mesonotum may be arranged differently from metanotum. Small paired areas are often set off at the anterior angles of the notum; they have been named the scutum I by CRAIGHEAD (1916). In Cerambycinae, Apatophyseinae and, as a tendency, also in most Prioninae, an anterior portion of mesonotum (including praescutum and anteromedial parts of both halves of scutum I) separated from mesothorax and very closely associated with prothorax as a transverse fold behind posterior margin of pronotum. This fold is called postnotal, or the postnotum, and the remaining part of mesonotum is then of other proportions and mostly distinctly shorter, both in comparison with metanotum. Separate postnotal fold absent in the Cerambycine

Plate 9: A — *Byrrhus* sp. (Byrrhidae), diagrammatic illustration of body areas (thorax and first abdominal segment). B — Cerambycidae, dtto. (drawn essentially from Lepturinae). 1 — pronotum, 2 — lateral furrows, 3 — sublateral impression, 4 — praescutum, 5 — scutum, 6 — scutellum, 7 — scutum I, 8 — postnotum, 9 — scutal plate, 10 — parascutum, 11 — alar lobe, 12 — spiracular area with abdominal spiracle, 13 — epipleurum, 14 — mesothoracic spiracle, 15 — rudimentary metathoracic spiracle, 16 — pleural tubercle, 17 — pleural disc, 18 — episternum, 19 — epimeron, 20 — pleurum (preceding two areas fused), pleural lobe, 21 — coxa, coxal lobe, 22 — coxosternum, 23 — praesternum (in prothorax: 23a — mediopraesternum, 23b — lateropraesternum, 23c — anterior praesternal lobe), 24 — basisternum (24a — mediobasisternum, 24b — laterobasisternum), 25 — sternellum, 26 — sternellar fold, 27 — furcal pits, 28 — spinasternum, 29 — pit of rudimentary spina. (Some of the structures can be found only on Plates 10, 11 or 12.)

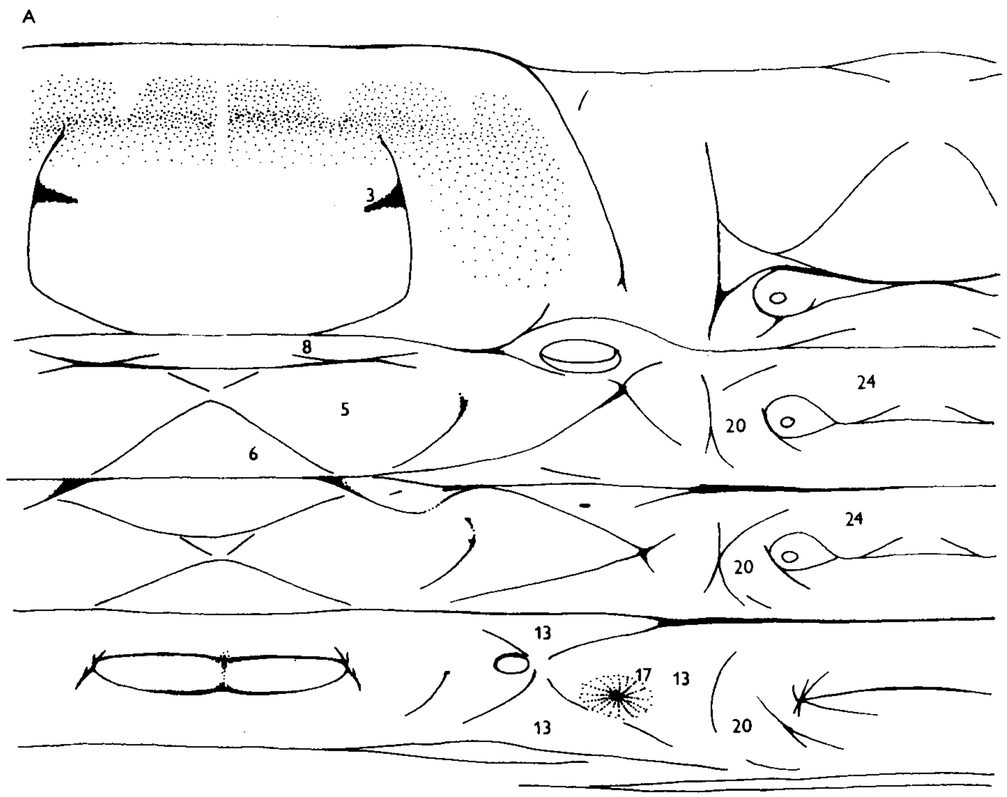


Plate 10: A — Prioninae, diagrammatic illustration of body areas (thorax and first abdominal segment, drawn essentially from *Ergates*). B — Cerambycinae, dtto. (drawn essentially from *Cerambyx*). For numbering see Plate 9.

tribe Methiini, however, it has been with all probability secondarily lost, perhaps fused with the pronotum - this requires further study, I had no material available for dissections. Development of the postnotal fold has been apparently connected with deep retraction of the head, which causes certain strong vertical thoracic muscles (originally attached at prothoracic-mesothoracic border between mesothoracic praescutum and scutum I) to move backward. Their dorsal attachments then cause a posterior postnotal border line. In Lamiinae where the head is often very deeply retracted, the narrow cranium passes between these muscles and does not cause development of the postnotal fold. The separate posterior pronotal area of the Lamiine genus *Batocera,* in my opinion, should not be called the postnotum (in the sense that it is probably non-homologous with the so named region of other Cerambycid larvae but originated by fragmentation of pronotum; cf. Fig. 12B). (Note: In improperly fixed contracted larvae the dorsal pterothoracic region is often so deformed, folded and some regions covered by another ones, that a study of this area is impossible without violent stretching of the cuticle.)

Notum laterally followed by so-called alar lobes, i.e. areas from which wings would originate (this can be plainly seen in prothetelic larvae where wing rudiments are often developed from this area). Alar lobes are separated from pterothoracic notum mostly by short indistinct impressions, or are fused with it, forming an entire tergum; the hierarchy »tergum = notum + alar lobes, notum = praescutum + + scutum + scutellum«, as proposed by CRAIGHEAD (1923), is thus used in the present paper. Alar lobes are ± triangular, with one angle pointed downwards, deeply bilobing the neighbouring ventrally area - the epipleurum, but not dividing it in two, as the pleurum (see below) has lost its contact with tergum (i.e. with alar lobes), and consequently the epipleurum is continuous along the whole segment. Anterior epipleural region bears the spiracle - very large in mesothorax, closed and rudimentary (rarely indiscernible) in metathorax. The mesothoracic spiracle, however, more often situated on the border between anterior epipleural region and the alar lobe. The spiracle-bearing region may be somewhat pushed into prothorax (Figs 10A, 12A), but the mesothoracic spiracle never makes an impression that it lies on prothorax (which is the case in some other larvae of Coleoptera or other Holometabola).

Pleurum rather reduced, consisting of two small areas half-surrounding the coxa, which are, however, almost or completely fused in the pterothoracic segments. These areas were named pre- and postcoxal areas (CRAIGHEAD, 1916), or pre- and posthypopleurum (CRAIGHEAD, 1923), but if more space was available, it could be easily shown that they represent the whole pleurum, the anterior one being the episternum, the posterior one - the epimeron. The epipleurum, which was considered to be a part of pleurum by CRAIGHEAD (»... epipleurum represents only a portion of the adult pleurum« - 1923, p. 19), must be regarded as a remaining part of membraneous lateral zone present before the pleurum was constituted. Thus the CRAIGHEAD'S terms precoxal area - prehypopleurum and postcoxal area - posthypopleurum (and

hypopleurum, if these two areas are fused) have been replaced by episternum, epimeron and pleurum respectively in the present paper. Legs are in Cerambycidae of little or no locomotory use, and this is probably why the pleurum lost its contact with (and support of) the tergum and why in meso- and metathorax the episternum is in most groups fused with the epimeron (in other words, the pleural sulcus has been lost, and the muscle attachments belonging to this sulcus are cumulated at dorsal margin of pleurum).

Although a part of leg, the coxa will be treated here, as it is ± built into the body wall, and, with a partial exception of a few species of Lepturinae with extremely (for the family) long legs, does not function as a leg segment; moreover, it often fuses with certain thoracic areas. Trochantin absent. Medial extremities of both coxae are in meso- and metathorax usually connected by distinct transsternal line dividing the sternum into an anterior (basisternum) and a posterior (sternellum) regions. Sternal endoskeleton (in the species dissected) absent. Basisternum laterally neighbours (and often fuses) with episternum, sternellum with epimeron. Basisternum in some groups divided by two curved anteriorly converging lines beginning about lateral extremities of the transsternal line into an unpaired mediobasisternum and paired laterobasisternum.

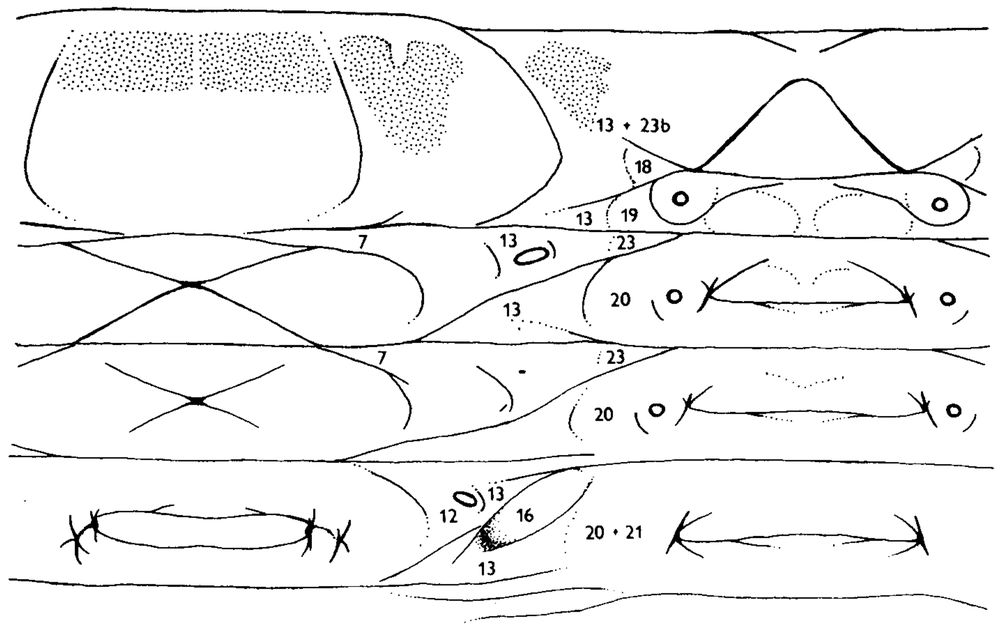
A weakly sclerotized or unsclerotized fold anterior to the basisternum and episternum of Coleoptera larvae is called the praesternum. In Cerambycid larvae, the pterothoracic praesternum is reduced in the middle, and only small lateral triangular areas can be found, often fused with epipleurum. (Fig. 9A of the *Byrrhus*-larva showing a fully developed praesternum.)

Various areas of pleurum and sternum may fuse one with another and/or with coxa, up to an entire venter with only the transsternal line preserved.

Prothorax always larger than meso- or metathorax (which are usually of about same size). Pronotum usually ± entire, not divided by any distinct transverse lines. Posterior half often somewhat raised, may be characteristically sculptured. Pronotum laterally delimited (at least in its posterior half) by distinct ± longitudinal grooves, called the lateral furrows (except for most Lepturinae and some Lamiinae where they are vestigial or absent). Sometimes (very distinctly in some Lamiinae) there are two supplementary oblique impressions in the pronotal area, caused by certain head muscles; they are called the sublateral impressions in the present paper.

Areas neighbouring laterally with the pronotum are called the alar lobes. Although some objections may arise against using the term in prothorax (in accordance with different theories of the wing origin and because it is not sure as to whether the lateral furrows are serially homologous with lateral limits of pterothoracic nota -- in fact I believe they are not), I prefer not to replace the above term, since it is not clear anyway which term should be used (mediotergum and lateroterga?). Anterior margin of pronotum and alar lobes almost always with a ± distinct transverse pigmented sclerotized band, the alar lobes usually more finely sclerotized also behind that band. Pronotum may be occasionally largely finely sclerotized as well. The

A



B

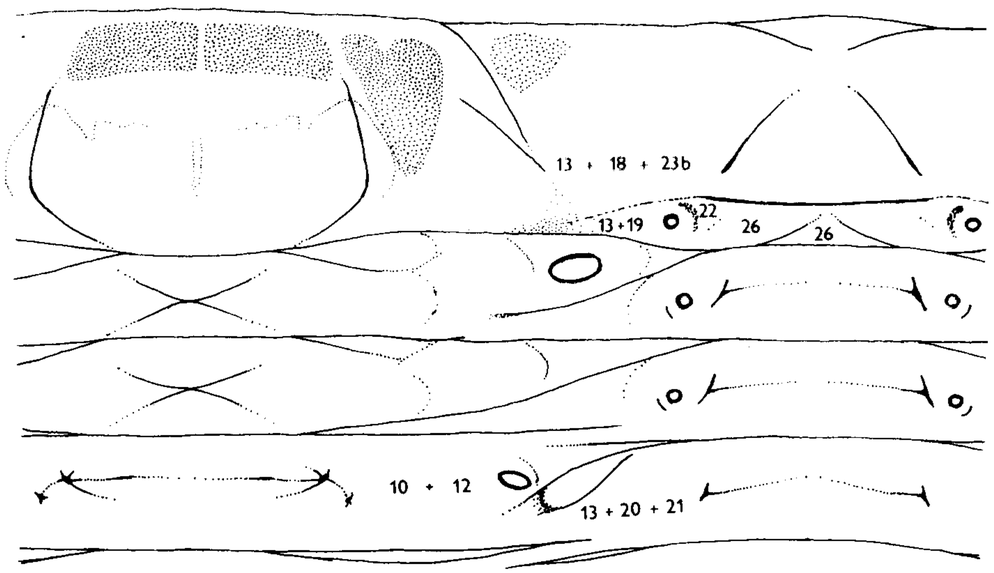


Plate 11: A — Aseminae, diagrammatic illustration of body areas (thorax and first abdominal segment, drawn from *Saphanus*). B — Aseminae, dtto. (drawn from *Tetropium*). For numbering see Plate 9.

pigmented band is always narrowly interrupted in the middle (cleavage line), in most Cerambycinae and Aseminae it is also interrupted by the lateral furrows. Anterior margin of the band has often a very characteristic outline.

Epipleurum developed as a simple longitudinal fold originally narrowing anteriorly (if ventrally delimited), so that the alar lobes ± touch the praesternum at the anterior margin of prothorax. Proepisternum and proepimeron separated one from another, mostly do not fuse even if some of them is fused with other areas (see below). The upper part of the pleural sulcus may (e.g. in Prioninae) protrude inside the body cavity as a small apodeme. Episternum (when fully defined) projecting anteriorly into a sharp angle, which, however, does not apparently belong to the true episternum and has been attached to it later.

Greatest changes in comparison with the CRAIGHEAD'S terminology have had to be made in prothoracic sternum. The transsternal line is absent in prothorax. In most generalized situation (e.g. all Lepturinae) the lines separating medio- and laterobasisternum are, on the contrary, very distinct, and each half of the latter is ± fused with the coxa of its side. Till now the laterobasisternum has been treated as a part of coxae, and consequently the fore coxae have been considered very large, in some groups »almost touching one another medially«. In fact the prothoracic coxae are mostly a little smaller than the pterothoracic ones. The area of fused coxae and laterobasisternum is called the coxosternum (or two halves of the latter) in the present paper.

Mediobasisternum is, on the other hand, fused with sternellum. This region of complex origin has been considered to be the sternellum, which term is no longer available. In the present paper it is called the sternellar fold, as the terms »mediobasisternum« and »sternellum« lost practical sense because of fusion of the two regions. (Thus, the term »sternellar fold« is used by us in a different sense than by CRAIGHEAD, 1923!)

The whole large anterior region is homologous with the propraesternum of other Coleoptera larvae (it is, however, difficult to say to what extent it is homologous with the meso- and metathoracic praesterna). In Cerambycidae the propraesternum is very large due to ± retracted head, and it is originally divided into ± triangular medial region, the mediopraesternum, and paired lateral areas, the lateropraesternum (both halves of which are, however, narrowly joined anterior to the mediopraesternum). The mediopraesternum has been till now regarded as the eusternum (i.e. the basisternum in the present terminology) of prothorax.

Prothoracic sternal endoskeleton absent, or there may be rudimentary spina visible externally as a shallow pit between pro- and mesothoracic sterna, rarely with vestigial transverse spinasternum present on both sides of the spina (mainly in some Lepturinae; Fig. 9B).

Modifications: Prothoracic sternum, pleurum and epipleurum as described above can be found in Lepturinae, Necydalinae and nearly so also in Apatophyseinae. In other groups, various fusions and modifications occur.

Parandrinae and Prioninae: Very complete situation. The border line between epipleurum and lateropraesternum absent, but a new one (never complete anteriorly) developed ventrally from the original one, in other words, a lateral portion of lateropraesternum moved to and joined with the epipleurum. A similar situation occurred parallelly in some highly derived Cerambycinae. Moreover, the mediopraesternum of Parandrinae with secondary anterior and lateral border lines (see general morphology of Parandrinae).

Aseminae: In some groups rather complete situation (Fig. 11A). Epipleurum fused with lateropraesternum. In Asemini the episternum poorly defined. Coxae, laterobasisternum, sternellar fold and epimeron tend to fuse into one transverse fold, and there is also a distinct tendency of a posterior portion of epipleurum to fuse with this fold, which is the case in most Cerambycinae (see below).

Apatophyseinae: A similar tendency, otherwise these larvae exhibit a very complete original situation. Lateropraesternum fused anteriorly with epipleurum.

Cerambycinae: Coxae, laterobasisternum, sternellar fold, epimeron and usually a posterior portion of epipleurum almost or completely fused into a transverse fold reaching on each side to the upper extremity of mesothoracic spiracle (Fig. 10B). (This fold is called the sternellar fold by CRAIGHEAD, 1923.) Lateropraesternum fused with epipleurum except for the tribe Cerambycini, sometimes episternum fused with this area, too. Border between latero- and mediopraesternum occasionally also lacking.

Lamiinae: Legs vestigial or absent, coxal area, laterobasisternum, sternellar fold and often epimeron fused. Epipleurum, lateropraesternum and episternum fused. Posterodorsal angle of epipleurum in some groups separated and joined with alar lobe. Original border line between medio- and lateropraesternum absent or very indistinct (the only Lamiine larvae I have seen to have this line fully preserved are those of *Somatidia* spp. from New Zealand, Fig. 12C). In many Lamiinae, however, another similar line was developed, dividing praesternum into ± half-circular medial region and two lateral regions narrowly joined anteriorly (Fig. 12A). The resulting situation is rather similar to the original one, and names for the two regions have not been therefore changed, but it must be kept in mind that these areas are not fully homologous with the latero- and mediopraesternum of other subfamilies, since the »new« line lies out of the original one and the »new« mediopraesternum therefore includes a portion of the original lateropraesternum (this can be demonstrated, among other, by muscle attachments - the »old« line was caused exclusively by certain head muscles and the »old« mediopraesternum has no inner muscle attachments, while the »new« line caused laterally by certain originally episternal muscles, and the attachments of the head muscles responsible for the original line are scattered inside the »new« mediopraesternum).

For more detailed information and some very specialized cases (e.g. the *Agapanthia*-complex in Lamiinae) see the subfamily and generic descriptions.

Legs are generally short to vestigial or absent, only in some Lepturinae longer and

of locomotory or clasping function. Reduced legs may be perhaps of some use as a sensory appendage. Coxa was for the practical reason treated with thoracic sternum. The distal leg consists originally of four segments (trochanter, femur, tibiotarsus, praetarsus with one claw), having consequently full number of segments of Polyphaga-leg. (Note: We consider the term »tibiotarsus« correct for the penultimate segment beyond any doubt. The terms »tibia« and »tarsungulus« can be on no account accepted. All transitional situations between larval and adult-type leg can be found in prothetelic larvae (see below), depending on the degree of prothetely, and the tarsus is clearly derived from the penultimate larval segment.)

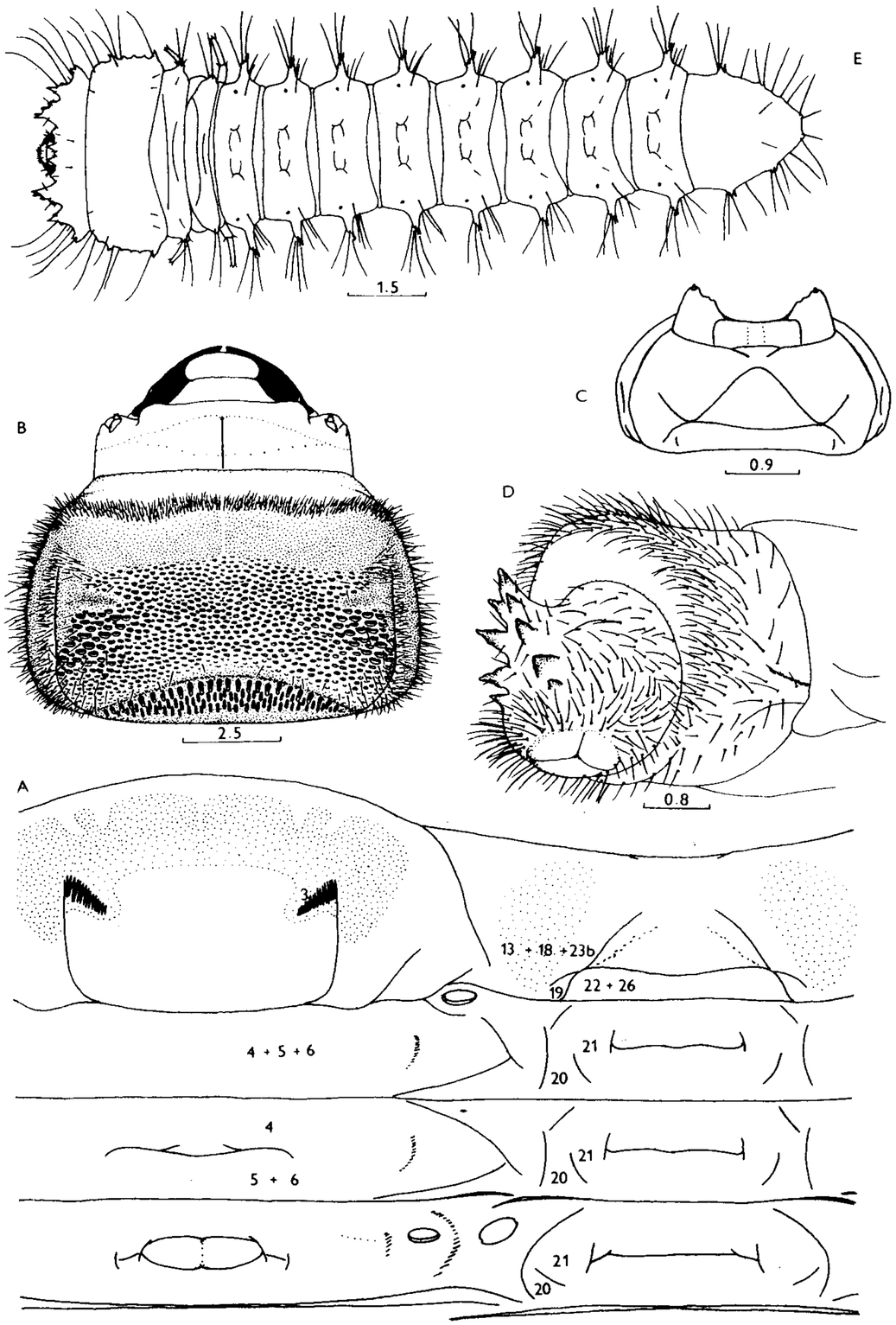
Ten distinct abdominal segments, including anal tubus, or the latter may be ± fused with segment 9. Special locomotory structures, so-called ambulatory ampullae, developed on segments one to six or seven, both dorsally and ventrally. In some *Agapanthia*-type Lamiine larvae the ventral ampullae (or even some dorsal ones, too) are absent due to special type of locomotion, e.g. in stems of herbaceous plants. Ampullae on segment 8 absent or entirely vestigial, except for the aberrant Lepturine larvae of the genera *Apiocephalus* (Fig. 12E) and *Capnolymma* with eight well developed granulate dorsal ampullae (granules not figured).

The dorsal and ventral intersegmental zones do not meet exactly one another in abdomen, the dorsal one being moved forward compared with the ventral one (very far in some long extended larvae where developed ± distinct secondary segmentation), and as they overlap one another in dorsoventral direction, the ability of telescopic movements (shortening and lengthening) of the abdomen may be very great, particularly in some extended and/or quickly moving larvae. Also the possibility of curving of the body is remarkable, particularly in the horizontal plane (because of the intersegmental zones overlapping laterally), and the larvae are able to turn in unbelievably narrow galleries. Only some Lepturine larvae are able to perform caterpillar-like movements when placed out of their galleries.

It is difficult to homologize individual regions of abdominal tergum with those of the pterothoracic tergum. Dorsal region of the ampulla-bearing segments mostly divided by two ± complete transverse lines joined laterally by one short longitudinal impression on each side, thus inclosing a transverse area called the scutal plate. Lateral impressions (which are outmarks of attachments of strong retractor muscles of the dorsal ampulla) may be divided in two in accordance with the retractors divided in two strands - this is the case in Lamiinae, Necydalinae, most Aseminae (Figs 11A, B, 12A). The pattern may be furthermore modified.

The anterior transverse line seems to be homologous with the praescuto-scutal line of pterothorax, the posterior one may be homologous with the scuto-scutellary line

Plate 12: A — Lamiinae, diagrammatic illustration of body areas (thorax and first abdominal segment, drawn essentially from *Saperda*). For numbering see Plate 9. B — *Batocera rubus* (Lamiinae, Oriental Region), head (outline) and prothorax, dorsal view. C — *Somatidia longipes* (Lamiinae, New Zealand), outline of cranium and prothorax, ventral view. D — *Uracanthus cryptophagus* (Cerambycinae, Australia), abdominal segments 9 and 10, posterolateral and slightly ventral view. E — *Apiocephalus punctipennis* (Lepturinae, Africa), larva, dorsal view.



(at least in its medial section). The terms »praescutum« and »scutellum« are therefore used for areas anterior and posterior to the scutal plate respectively. In abdomen, these areas are, however, not defined laterally, fusing on each side with paired lateral region of notum, the so-called parascutum, incompletely set off by the two longitudinal impressions. Scutal plate plus parascutum are regarded as homologous with pterothoracic scutum.

Dorsal locomotory protuberance - the dorsal ambulatory ampulla - includes the whole scutal plate, a posterior portion of praescutum, an anterior portion of scutellum and medial portions of both halves of parascutum. Ampulla usually shallowly to deeply impressed medially, sometimes even bilobed. Its surface always distinguished from the surrounding cuticle, often with various special developments.

Parascutum separated by at most fine indistinct curved lines from the neighbouring spiracular areas, which are considered ± homologous with alar lobes of pterothorax. At the ventral border of spiracular area lies in segments 1 to 8 the abdominal spiracle.

Epipleurum of segments 1 to 9 forms in most Lepturinae, some Necydalinae and some Lamiinae a protuberant longitudinal fold, anteriorly and posteriorly ± projecting upwards along the curved border line with spiracular area. In other groups the epipleurum protuberant only in a few posterior segments (but at least in segments 8 and 9, mostly also 7). In other segments the dorsal epipleural border ± disappears and the epipleurum ± fuses with spiracular area; then often developed a ± distinct oblique line dividing the fused area in two parts of mixed origin, the anterior one bearing spiracle.

Anterior portion of epipleurum often with a ± pronounced oval or subcircular protuberant area - the pleural tubercle (should be more correctly called the epipleural tubercle, the above term originates in CRAIGHEAD's concept of the epipleurum being a portion of the pleurum). Pleural tubercle occasionally (almost exclusively in Lamiinae) with minute sclerotized dot or pit at one or both extremities.

In some groups (most Prioninae, some Cerambycinae), small areas of cuticle with different sculpture (mostly concentrical to the central point) can be found in epipleural region of a few anterior abdominal segments (at most 1 to 6). The structure is called the pleural disc (Figs 10A, B). The central point corresponds with dorsal pit of the tubercle of Lamiinae.

Pleural tubercles are usually indistinct, and pleural discs may be only distinct, on segments with non-protuberant epipleurum. Both these structures are in relation to chordotonal organ which is attached in the central point (the dorsal extremity of the tubercle, the dorsal pit of the tubercle of Lamiinae), and stretched anteroventrad to a small cuticular infolding (the ventral extremity, the ventral pit of Lamiinae). For more details see HESS (1917).

Unlike the tergum, the ventral region (below the epipleurum) of an abdominal segment seems to be easily homologizable with that of pterothoracic segments. Triangular praesternum further more reduced and often fused with epipleurum.

Transsternal line mostly developed as in pterothorax, separating anterior basisternum from posterior sternellum. Basisternum usually undivided. Sometimes (e.g. in many Prioninae) there is a less distinct incomplete second transverse line posterior to the original one. A short ± longitudinal impression (rarely doubled) at each extremity of the transsternal line incompletely separating so-called coxal lobe, regarded as homologous with thoracic coxal region. A separate region lateral or posterolateral to the coxal lobe seems to correspond with thoracic pleurum, unusual as it might seem to use this term in abdomen. The region here called the pleural lobe; it may be rather reduced, or fused with either coxal lobe or epipleurum.

Ventral ambulatory ampulla includes a posterior portion of basisternum, an anterior portion of sternellum and medial portions of both coxal lobes.

Eighth abdominal segment without ampullae, epipleurum always protuberant, transsternal line and lines dividing notum obliterated. An exception (dorsal ampulla 8 present) see above.

Ninth segment simplified, with entire tergum, protuberant epipleurum without pleural tubercle, and entire venter (all ventral areas fused). Hind margin of ninth tergum occasionally with sclerotized structures collectively called the caudal armature. The latter may be paired or unpaired. Paired caudal armature (mostly two small sclerotized spines) apparently homologous with the urogomphi of other Coleoptera larvae. The unpaired armature (mostly a single medial spine) may be either homologous with urogomphi (apparently in Lamiinae where fusing of the urogomphal spines may be demonstrated in some *Parmena*-larvae), or may represent a newly developed structure, perhaps several times independently (probably the unpaired caudal spines of Lepturinae). Urogomphi may be either present or absent in the first instar larvae (present e.g. in *Saphanus,* Aseminae), the caudal spine of Lepturinae always absent from the first instars.

Anal segment (anal tube) mostly short, directed caudad or slightly ventrad, only in some depressed subcortical Lepturine larvae pronouncedly ventral and used to some degree as a pseudopod. Anus mostly triradiate, i.e. surrounded by three so-called anal lobes, or anal papillae (one dorsal and two lateroventral). These papillae are mostly ± distinctly separated from the anal tube by a slight circular impression; they may represent rudiments of the eleventh abdominal segment. In some Lamiinae the ventral radius of the anal opening is reduced or wanting, the anus thus becoming a transverse cleft. Rarely anal tube with secondary sclerotizations (very remarkable e.g. in the Australian genus *Uracanthus,* Fig. 12D). Abdominal segments other than 9 and 10 very rarely bear macroscopic sclerotized structures.

Spiracles: Cerambycid larvae are of peripneustic type (mesothoracic + 8 abdominal functioning spiracles), metathoracic spiracle closed, rudimentary, externally visible only as a small ± sclerotized dot, or indiscernible. Mesothoracic spiracle almost always at least slightly larger than abdominal ones, lies in the anterior region of epipleurum or on the border between epipleurum and alar lobe. Occasionally (e.g. in some Cerambycinae) the spiracle-bearing epipleural area may be fused with

alar lobe. Abdominal spiracles present on segments 1 to 8 and no case of reduction is known to me.

Spiracles are elliptical to subcircular in external view, opening by a ± vertical slit (sunken under the surrounding cuticle) leading into a roomy spiracular chamber. Externally exposed spiracular structures ± sclerotized and pigmented, outer margin mostly with two to many characteristic structures, the so-called marginal chambers (e.g. Fig. 261), of varying size and unknown function.

Microscopic spines and similar locomotory sclerotizations: Various body areas (most often certain regions of thoracic nota and sterna, incl. coxae, and of ambulatory ampullae) may be covered with microscopic cuticular spines of non-setal microtrichial origin (Fig. 13A), which make the body surface rough. Sclerotizations of this type may occasionally become larger, up to areas covered with macroscopic sclerotized »grains«, mostly with sharp raised edges (e.g. Fig. 12B).

Granulation: Ambulatory ampullae, pterothoracic sterna and sometimes nota as well may be »granulate«, i.e. with cuticle divided into small ± protuberant areas - -the granules. This is another adaptation for locomotion in galleries.

Variability

Growth variability: Young larvae differ substantially from the older or »mature« ones. This variability must be always kept in mind during determination. Some main differences are as follows:

- generally, young larvae are more uniform, do not have fully developed characteristic habitus of older larvae, particularly if these are adapted to some less typical way of life
- setae in smaller number, esp. if they are dense in older larvae
- cranial and other proportions may change considerably
- sculpture of cranium and mandible ± lacking
- all pigmentation paler than in older larvae (except when there is an inactive final instar, as in some Callichromini of Cerambycinae or some Phytoecia of Lamiinae, which is then poorly pigmented), pigmentation of certain areas may be entirely lacking
- smaller number of epistomal setae if there are more than six setae in mature larvae
- form of epistoma gradually changes during ontogenetic development
- in Lepturinae the transfrontal line indiscernible even if distinct in mature larvae
- medial frontal line often continuous along the whole frontal length even if in mature larvae interrupted or shortened
- stemmata usually better developed, present even in some groups where they are indiscernible in mature larvae
- subfossal process absent or relatively smaller
- proportions of segments of antennae and palps change, in young larvae segments relatively broader and shorter, ultimate palpal segments relatively larger than in later instars
- marginal chambers of spiracles relatively larger and in smaller number
- microscopic spines relatively larger and not so numerous, often in other (usually greater) extent as to the relative area covered

etc.

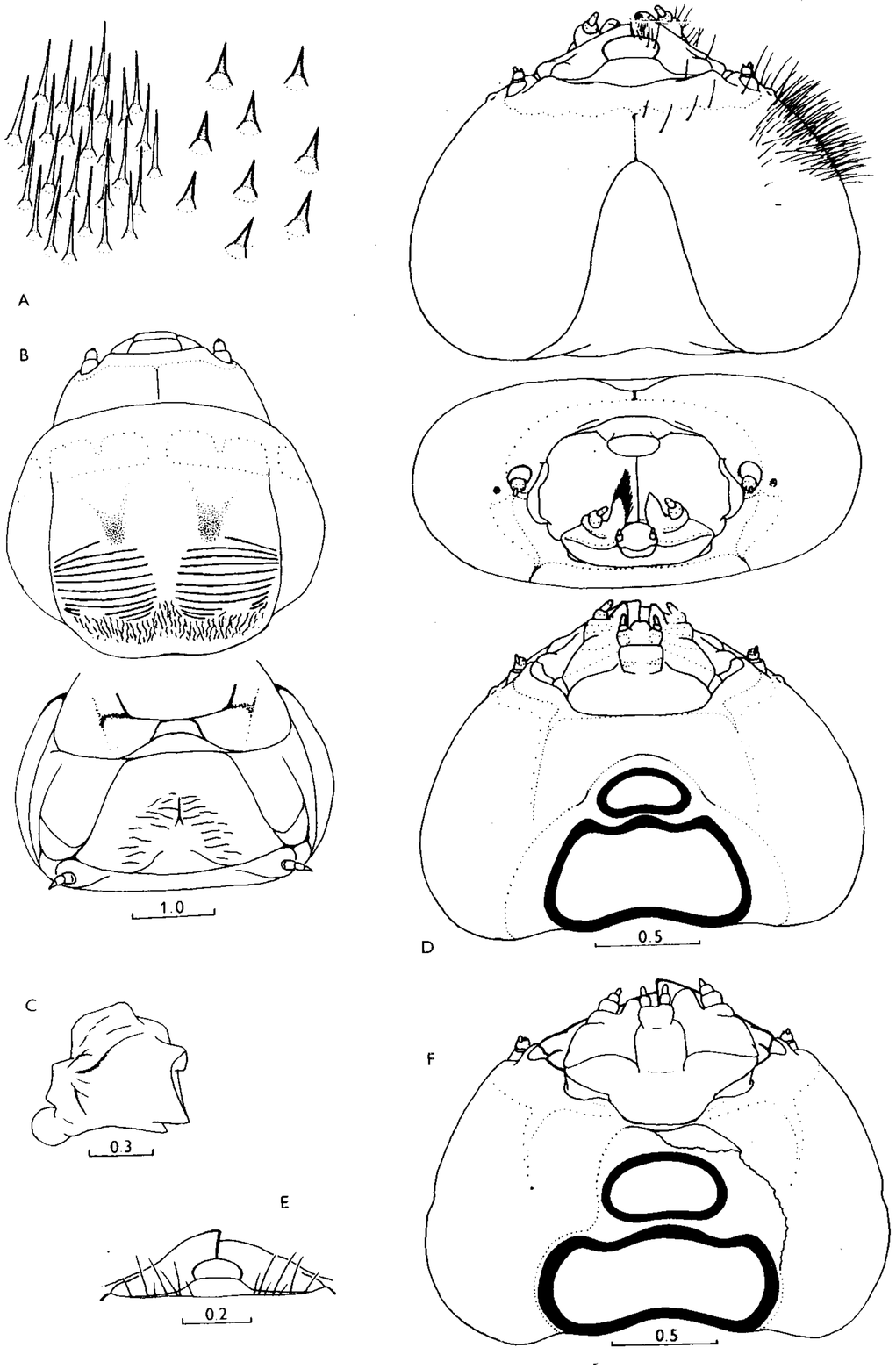
Individual variability may be very great in Cerambycid larvae, and it is also multiplied by the extreme individual variability of size. Particularly exceptionally great individuals may differ substantially by stronger sclerotization, more coarse sculpture, relatively denser setae etc., as well as in many particular characters. The individual variability is not necessarily continuous! It is difficult to draw exact border line between »normal« and »abnormal« variability. E.g. it seems that if a larva has been disturbed shortly after moult and forced to escape, use its mandibles etc., it may result in changed cranial sculpture, proportions and other details. Mandibles deserve special mention, being extremely variable particularly in the type I. Moreover, as a working tool they are subject to extensive abrasion and towards the end of an instar they may become much shorter and with practically all sculptural details obliterated.

Geographical variability causes the same difficulties as in any other similar group and does not need special mention. I must point out that in almost no species with more extensive range we have had available larval material from at least most of the region of its distribution. If material from two or more distant localities was available, then at least slight statistical differences were often found.

At present we are unable to externally distinguish sexes of the larvae, therefore the contribution of sexual component to general variability remains unknown.

Some species or groups of species (some Callichromini of Cerambycinae, some *Phytoecia* of Lamiinae) have been revealed to have the last larval instar (apparently always diapausing) strikingly different from the preceding ones. Transformation into this instar seems to take place in the previously prepared pupal chamber and the last instar larva apparently does not construct further galleries, perhaps it does not feed at all. In general it is always much less sclerotized and more robust.

The untimely occurrence of certain pupal (adult) characters in larvae (the prothetely) can be rarely observed in larvae collected in the nature but can be rather frequently induced in breedings by unsuitable conditions (in the nature the larvae in unsuitable conditions usually soon die under influence of various factors which can be in breedings ± restricted). The appearance has been usually ascribed to a failure of the hormonal balance. According to the degree of prothetely the larvae may have wing rudiments, legs present in legless larvae, tibiotarsus divided into tibia and tarsus, two claws, more antennal segments, rudiments of external genitalia, stemmata ± replaced by compound eye etc. Although extremely interesting from the standpoint of general morphology, these larval forms are aberrant and quite irrelevant as far as descriptions are concerned. Prothetelic forms have been occasionally erroneously described as a regular praepupal stage (e.g. CHEREPANOV, 1984, p. 140, *Exocentrus marginatus*). I must point out that not a single case of regular prothetelic praepupal form is known to me, although in some groups they may be induced much more easily than in others (e.g. the last larval instars of some Callichromini - see above - showed great tendency to develop prothetelic forms). I have seen prothetelic larvae of all subfamilies except for Parandrinae and Apatophyseinae,



but this is undoubtedly due to the scarcity of larval material I have examined of the latter two subfamilies.

Short differential characteristic of larvae of the Cerambycidae

Cerambycid larvae can be distinguished from other larvae of Coleoptera by the following combination of characters: Free labrum developed. Mandibles without molar armature and without any articulated appendages. Endocarina almost always present. Exposed coronary suture absent, dorsal head retractors attached at frontal base, but (with the exception of Necydalinae and most Lepturinae) epicranial halves widely fused behind this attachment due to cuticular duplicature (this situation occurs very rarely in other Coleoptera). Hypostomal ridges and consequently hypostomal lines present except for a few Lamiinae. Hypopharyngeal bracon and hypopharyngeal sclerome absent. Sclerotized gula or gular area present. Galea and lacinia fused without traces into mala. Body almost unsclerotized. Legs (with very rare exceptions) reduced and without locomotory function, or absent. First seven abdominal segments (or at least some of them) with at least dorsal ambulatory ampullae.

Some problematic larval forms

1) *Anoeme nigrita* CHEVROLAT, 1855: Although generally a Prionine-type, the larvae differ at least as much from the Prioninae as do the larvae of *Parandra*. Main differences from all (or at least typical) Prioninae as follows: Postcondylar, frontal and epistomal carinae absent. Frontal lines practically indiscernible along whole length, sclerotization of mouthframe uninterrupted. Medial pair of epistomal setae small, far distant from clypeal border, almost as in Cerambycinae. Mandibles quite different from all Prioninae or *Parandra* (Fig. 13C), with sharp supplementary tooth below apex, type II-keel extremely small at dorsal angle. Pronotum (Fig. 13B) expanded backwards, posterior half with coarse transverse ridges, each groove between them with a row of short setae. Prothoracic venter (Fig. 13B) uniquely divided; sternellar fold much reduced, mediopraesternum not defined, praesternum divided by two oblique lines reaching anterior margin. Anterior praesternal lobe large, distinctly

Plate 13: A — Microtrichia (left) and microscopic spines (right), which are in fact short sclerotized microtrichia, under great magnification. Even if certain very large microtrichia (on ligula etc.) of some species may resemble small setae, they may be readily identified due to lack of basal articulating structures of a seta. B — *Anoeme nigrita* (Africa), outline of head and prothorax, dorsal (upper) and ventral (lower) views. C — *A. nigrita*, right mandible, apical and slightly lateral view. D — *Opsimus quadrilineatus* (North America), head, dorsal (upper), anterior (middle) and ventral (lower) views. (Setae figured only on the right half in the dorsal view, and on the right mala in the anterior view.) E — *Tessaropa tenuipes* (Cerambycinae, Methiini, North America), anterior part of head in dorsal view, showing multiplied epistomal setae. F — *Oeme hirsuta* (*O. rigida deserta* according to LINSLEY, 1962b) (Cerambycinae, Methiini, North America), outline of head, ventral view (left half of postgular lobe not removed).

separated from praesternum. Ambulatory ampullae distinctly microspiculate except for areas along impressed lines which are smooth and very distinctly rugose.

Material: 1953 Kenya, Ngong, two larvae ex dead *Ficus*, J. C. M. Gardner lgt., coll. British Museum. These larvae were described and figured by DUFFY (1957) as *Anoeme* sp. Later on (1980) he assigned them to *A. nigrita* on the base of the study of an additional larva associated with adult.

2) *Dorcasomus gigas* AURIVILLIUS, 1914: Despite DUFFY (1957, 1980), the genus *Dorcasomus* cannot be retained in Lepturinae. The larvae are distinctly related to *Apatophysis* and must be preliminarily classified in the Apatophyseinae (which, as has been already pointed out in the chapter on higher classification, have no direct relation to Lepturinae). For my opinion concerning the Ethiopian Lepturine-like forms see the same chapter.

Main differences from *Apatophysis:* Projecting epistoma absent, epistomal margin only abruptly bulged above clypeus. Medial pair of epistomal setae moved far backwards, almost as in Cerambycinae. Three distinct main stemmata present. Subfossal process ± absent. Mandible with small type II-keel present at dorsal angle. Ventral sclerite longer, metatentorial pits distinct, metatentorium pronouncedly internal (Fig. 14A). Body devoid of microscopic spines, ampullae finely granulate. Largest available larva 55 mm.

Material: 1953 Uganda, two larvae ex *Bersama* sp., J. C. M. Gardner lgt., coll. British Museum; one larva with no data, coll. British Museum.

DUFFY (1980) has described larvae of another species, *D. delergorguei* GUÉRIN-MÉNÈVILLE, 1845, which appears to be very similar to *D. gigas*.

3) *Opsimus quadrilineatus* MANNERHEIM, 1843: This curious larva has been described by CRAIGHEAD (1923). It is briefly characterized as follows: Body moderately elongate, broadest at prothorax. Cranium (Fig. 13D) transverse, epicranial halves fused along whole length, dorsal doubled region protruding deeply into frons. Frontal lines indiscernible. Medial frontal line distinct. Separate epistoma absent, epistomal margin and epistomal setae of Cerambycine type. Clypeus abruptly narrowed, although its lateral extremities reaching to mandibular articulations are broader and more distinct than in most Cerambycinae. Labrum small, moderately transverse. One main stemma with distinct pigment spot. Epicranium anteriorly very hairy. Antennae short, three--segmented, main sensillum conical. Typical rounded spoon-like Cerambycine-type mandible. Labiomaxillary complex rather remarkable. Cardo extremely reduced and pushed laterad by expanded connecting lobe, labiomaxillary base thus attached to cranium along almost whole width. Maxillary palp two-segmented (segments 2 and 3 fused), palpiger and first palpal segment lacking processes. Mala uniquely shaped, flat, lanceolate, with dense regular long marginal setae, curved upwards along apical mandibular face (Fig. 13D). Ligula broad, labial palps separated by more than twice their width. Ventral sclerite medially short, in hypostomal region

rather long, metatentorial arms slender, pointed moderately obliquely inside cranial cavity yet well visible in ventral view, metatentorial pits almost absent.

Pronotum delimited by long deep lateral furrows. The single available larva is so contracted that a study of pterothoracic and posterior prothoracic region is difficult. Postnotum apparently present. Prothoracic venter seems to be extremely modified. All parts incl. epipleurum ± fused except for distinct anterior and lateral limits of mediopraesternum which are extended backwards and reaching posterior prothoracic margin. Pterothoracic ventra divided only by transsternal line. Legs absent.

Ampullae on segments one to seven, non-granulate. Dorsal ampullae with three impressions on each side and a median furrow, transverse lines absent. Ventral ampullae with two impressions on each side, transsternal line present. Distinct pleural discs absent. Epipleurum protuberant on segments 7 to 9. Ninth segment small, caudal armature absent. Anus triradiate.

The genus *Opsimus* has been placed either in Aseminae or in Cerambycinae (cf. LINSLEY, 1962, p. 5). The peculiar larva causing a lot of difficulties since its description. CRAIGHEAD (l. c.) included *Opsimus* in the Aseminae, stating that it »forms a distinct transition between the Aseminae and the Cerambycinae« (p. 35). I do not share fully this opinion. The larva has not a single primitive character compared with the supposedly primitive Cerambycinae (in my opinion the tribe Cerambycini and some allied groups) - as a whole the larva is strongly derived. All the characters considered by CRAIGHEAD to be Asemine (broadly attached labiomaxillary complex, mala borne ± on palpiger, but not as distinctly as in the Aseminae) are in details different from the latter subfamily, and are not restricted to that subfamily. The pattern of ambulatory ampullae is strikingly different from typical Cerambycinae, but it also differs from typical Aseminae. Dense epicranial setae also cannot be taken as a definite Asemine character. The larva has some striking unique features (mala, prothoracic venter). Such character as the two-segmented maxillary palp occurs in no known Asemine larva, but can be found in some Cerambycinae. Some distinct and, as far as known, unique Cerambycine apomorphies are present (mandible, clypeus). Also the postnotal fold seems to be present, although from the single contracted larva I am not sure. Therefore I agree with at least preliminary inclusion of the genus in the Cerambycinae, but on no account as a primitive member.

Material: Canada, British Columbia, Vancouver Island, Sidney, one larva from heartwood of Douglas fir (*Pseudotsuga*), G. A. Harvey lgt., coll. U. S. National Museum, Washington.

4) The tribe Methiini (incl. Oemini): These undoubtedly Cerambycine larvae have two peculiar characters. The postnotal fold is absent (not known in any other Cerambycinae), but various indications suggest it has been secondarily lost, perhaps fused with pronotum. Unfortunately I have no own material available for dissection. Secondly, the exposed gular region is very short due to large postgular lobe and the submentum expanded backwards (Fig. 13F). Some Methiini have the epistomal setae

multiplied (Fig. 13E) which is not known to me in other Cerambycinae. Generally the larvae seem to show certain similarities with the Molorchini.

Material available of the genera *Oeme*, *Methia*, *Tessaropa* and *Styloxus* (coll. U. S. Natn. Museum, Washington, and Ohio State University, Columbus). On the other hand, some other genera included occasionally in the tribe (*Malacopterus*) have nothing common with it, and *Vandykea* is an Asemine (see taxonomic chapter).

5) *Teledapus dorcadioides* PASCOE, 1871: Larvae not at my disposal. Described by GARDNER (1942) and DUFFY (1968) who both expressed no suspicion about the genus belonging to Lepturinae. The larva has an unique robust caudal process terminated by two pairs of sclerotized points (see DUFFY, l. c., and the illustration therein). Also the broad mala (GARDNER, l. c.) occurs rather rarely in the Lepturinae. The larvae used to be in the collection of the Forest Research Institute, Dehra Dun, India (cf. DUFFY, l. c.), but, according to a letter of Dr. A. Chandra, they are now absent from their collection. Neither they are housed by the British Museum (Natural History), and therefore I am afraid they have been destroyed or lost.

Short account of bionomics

All Cerambycid larvae, as far as known, are either endophytic (live inside plant tissues), or live in the soil. No free-living forms (defoliators etc.) are known. Therefore, with partial exception of a few Lepturinae (e.g. *Dinoptera,* and also some other genera larvae of which leave the wood and pupate in the soil), the larvae cannot be found freely in the nature, and cannot be obtained by practically any usual methods for mass collecting of insects (sweeping, beating, or various traps), neither they are sufficiently abundant at any site to be obtained by methods for collecting soil Arthropoda.

Immature stages of great majority of the Cerambycidae are connected with woody plants, either living or at almost any stage of deterioration except for highly decayed wood infested with »dark rots« (fungi which utilize mainly cellulose) which is usually free from Cerambycid larvae. Very few species are able to feed in the outer corky layer of the bark. Any part of the plant, both above and below ground level, may be infested, from large trunks up to thinnest twigs. Feeding in decomposing wood has been often considered the initial type.

However, some species feeding in highly decayed wood must be apparently considered at least partly mycophagous (this is clearly demonstrated by some Lepturinae, and the larvae of *Pseudovadonia livida* live freely in the soil with mycelium of the fungus *Marasmius oreades* which apparently constitute an indispensable food component). Certain Lepturinae, Cerambycinae and Lamiinae feed in herbaceous plants, perennial or annual, in stems or roots. Some Cerambycid larvae live in the soil, feeding on the plant roots externally. Finally, relatively few Cerambycidae are known to feed in generative plant organs (seeds, cones - *Paratimia*).

Eggs are relatively small, ± elongate oval, and usually are laid on the food substrate, either at specially prepared sites (typical in Lamiinae), or simply in crevices, old galleries, or on the surface. Only some root feeders are known to lay eggs in the soil, with the first instar larvae actively searching for the food source; the number of eggs is then rather great (e.g. *Stenocorus* of Lepturinae). Selection by female of ovipositing sites is of great importance since the larvae are usually incapable of leaving unsuitable food material and searching for a new one, except for some subterranean species which may tunnel extensively from root to root.

First instar larvae usually possess some special hatching devices. Most widespread seem to be lateral spines on some thoracic and/or abdominal segments, some species have special cranial or mandibular spines, and the larvae of *Saphanus piceus* (Aseminae) have been observed by the author to use also urogomphi for rupturing the chorion. Striking adaptations of the first instar larvae of *Agapanthia villosovoridescens* (Lamiinae), e.g. the dorsal prolegs, have been described by DUFFY (1952). First instar larvae, as far as known, feed and grow, being not an ephemerous instar known in some Coleoptera or other insects.

Number of larval instars usually unknown. It seems that four is the minimum possible number (four larval instars were reported for *Dectes texanus* by PATRICK, 1973, and may be probably also found in other quickly developing species from fresh living plant tissues). STARZYK (1977) found *Gaurotes virginea* to undergo five instars, SALIBA (1977) found six instars in *Cerembyx dux*. Apparently about five to seven should be the usual number. However, the number must be supposed higher in some species with long generation period, as well as in the cases of longevity (see below). We must also suppose unstable number of instars in species with individually variable development period.

The latter usually lasting about 1 to 3 years. Two generations a year are, at least in colder climatic zones, rare. On the contrary, numerous cases of longevity (up to several tens of years) have been recorded in some species feeding in dead ± solid wood (*Stromatium, Hylotrupes, Eburia* etc.), usually caused by utilization and following extreme dessication of the infested wood (as structural timber, furniture etc.). For an account see DUFFY, 1953.

Pupation takes place either in the food material or in the soil. As a whole it seems that pupation in soil is secondary in the Cerambycidae, occurring either in the species with soil-dwelling larvae, or in groups larvae of which live in conditions unfavourable for pupation (e.g. under very loosen bark). Also the tree-root feeders often pupate in the soil, which may be advantageous for adult emergence. However, in some groups pupating in the soil (e.g. the *Oxymirus-Anthophylax* group of Lepturinae) the reason is not clear, except when interpreted as a preserved primitive feature.

In colder regions, the overwintering stages may be the larva, pupa or adult. No reliable observation of overwintering eggs known to me. Most frequently the larvae overwinter (the last winter often as mature larvae in pupal cells, or even as pharate pupae). Pupal overwintering known to me in *Evodinus* of Lepturinae (apparently not all specimens) and in some Cerambycinae, e.g. some Callidiini or Molorchini.

Adult overwintering occurs in various groups, adults usually hibernate in their pupal cells. Known cases of true adult overwintering (outside pupal cells) include e.g. the Lamiine genus *Pogonocherus*.

As to the ability of Cerambycid larvae to digest various components of their food, the enzymatic set has been found rather wide (cf. LINSLEY, 1959, 1961), although relatively few species have been studied in that respect, most of them being typical wood feeders. (The apparently important recent account by CHARARAS, 1979, has not been available to me.) One of the most significant facts obtained is that at least some Cerambycid larvae are able to digest cellulose, and, moreover, all observations show that the cellulases are their own, not synthetized by some symbionts (cf. e.g. CHARARAS, 1981, CHARARAS et CHIPOULET, 1983, CHARARAS et al, 1983a), which seems to be rather uncommon case in insects, and may be taken as a proof of a long--term xylophagous specialization of the family. The symbiotic microorganisms (which have been found in many but not all the species studied, esp. Lamiinae seem to be deficient in symbionts), generally yeast-like, intracellular and found in special crypts on the midgut, have been never proved to exhibit cellulolytic activity, and are apparently responsible for synthesizing other enzymes, B-group vitamins, or perhaps helping in supplying available nitrogen. They are indispensable for larval survival; as far as known, they are present on the egg surface, and are ingested by the hatching larva. Consult e.g. CHARARAS et al., 1983b. The role of extracellular luminal intestinal microorganisms is not clear, beginning with whether (and then which, and in which species) they are really essential symbionts. They might, among other, fix the atmospheric nitrogen (see below). For an account of intestinal microorganisms of larval *Prionus laticollis* (with some physiological characteristics of the microorganisms isolated) see BENHAM, 1971.

The available nitrogen has been often considered one of the limiting factors in the development of the larvae feeding on dead plant tissues where the labile nitrogen--containing components (very sparsely represented even in fresh wood, more abundant in cambium layer) are subject to quick utilization by fungi etc. The fungi themselves may perhaps serve as a nitrogen source. In some other insects (MARTIN, 1984, KUKOR and MARTIN, 1983) it has been shown that the ingested fungi may also serve as a source of certain acquired enzymes used by the insect for its own digestion, and this may be partly also true for certain Cerambycidae living in fungus-rich substrate. The results of MISHRA, SEN-SARMA et SINGH (1985) suggest that the food nitrogen deficit may be compensated by the atmospheric nitrogen fixed probably by some of the microbial symbionts. A very interesting paper by FORCELLA (1982) showed a very simple yet previously not realized trapping effect for the nitrogen compounds caused by twig phloem girdling by females of *Oncideres cingulata* (Lamiinae), then ovipositing on the girdled twig.

Apparently for the same reason (shortage of nitrogen) many Cerambycid larvae will readily devour (not only kill) other insects (particularly some xylophagous larvae including Cerambycidae, and even own species) whenever the opportunity arises.

Hence the problem of equal dispersion of the larvae of one species, or even of different species, in the available space. In some species this is achieved by the ovipositing female, but more females may occasionally oviposit on the same site, and some species lay eggs in batches. It would be certainly important to avoid esp. intraspecific competition as long as it can be done. Sound is believed to play an important role (which is well known e.g. in bark beetles). Some sclerotized body areas may even serve as special »scrapers«. I have observed larvae of *Pogonocherus hispidus* (Lamiinae) producing loud noises by twisting their abdomen from one side to another pushing it simultaneously upwards, thus scraping the anal plate against the thin bark layer left above the subcortical gallery. This was observed in a densely colonized branch, and the sound may be of »territorial« purpose, helping the larvae to spread more equally in the branch. In fact the sounds resulting from normal larval activities are believed to be employed in the same manner (SALIBA, 1972). The abdominal epipleural chordotonal organs (see HESS, 1917) may be the sound receptors.

Problems of host selection and host specificity have been summarized by LINSLEY (1959, 1961). Generally it can be said that species living in dead and particularly decaying material are less host-specific than those feeding in fresh living tissues. Some observations show that certain oligo- or polyphagous species may exist in the nature in several host-strains to which can be applied the so-called Hopkins host--selection principle (cited after LINSLEY, 1961, p. 15): »Species which breed[s] in two or more hosts will prefer to continue to breed in the host to which it has become adapted.« This process may perhaps even result in sympatric speciation. The word »prefer« must not be apparently taken as concerning the ovipositing preference only - individual strains have been occasionally found to be evidently disadvantaged or even unable to establish in the host in which another strain of the supposedly same species bred succesfully (this is, however, a weak point of the whole matter; with our present taxonomic knowledge we can be seldom sure we are not dealing with two cryptic species, and I should also point out the sorrowful yet logical fact that the criteria of species as a taxonomic category have become more obscure instead of more clear in the recent years). The results with transferring half-grown larvae of a species from one host to another cannot be of course interpreted as that the strain may develop in the other host, as by far greatest mortality usually occurs during establishing of first instar larvae, not speaking at all about competition with other insects in the nature.

I do not feel myself obligated to comment extensively upon the economic importance of the group, as this has been done by many other authors. The destructivity of the Cerambycidae has been often intentionally overvalued to make the work of an author more »important« from the viewpoint of human economy. It must be stressed that relatively very few species are really seriously harmful to living healthy cultural plants or destructive to structural timber (the most notorious one in the cold and temperate Palaearctics being probably the Old House Borer, *Hylotrupes bajulus*). Great majority of the Cerambycidae do not cause any harm, and they are highly

beneficial in the process of decomposition of the wood, thus becoming an indispensable component of healthy forests in which they often occur in great variety of species. Unfortunately, most of the species seem to be highly sensitive to pollution, and they are rapidly disappearing from industrial regions. In addition, many Cerambycidae are tightly bound to natural forest or other formations and will not accept substitutional cultural ecosystems.

The family is worldwide, except for the climatically most extreme regions of the globe.

Key to subfamilies of Cerambycidae

Characters in square brackets are either not universally possessed, or not fully restricted to the group, or both, but generally will prove helpful.

1(2) Clypeus very narrow, with only slender basal arms reaching to mandibular articulations (Fig. 7B), these arms may be even ± sclerotized and fused with epistomal margin. Mandibular apex and dorsal angle ± lacking, mandible short, apically rounded, spoon-like (Fig. 8E). [Postnotum present except for Methiini. Usually four epistomal setae - medial pair pushed backwards far away from epistomal margin.] . . . . . Cerambycinae

2(1) Clypeus ± trapezoidal, filling entire space between dorsal mandibular articulations. Mandibles not rounded, with distinct (occasionally doubled) apex and ± distinct dorsal angle.

3(4) Legs absent, or minute one- or two-segmented rudiments present, visible only under great magnification. Cardo extremely reduced, labiomaxillary base firmly attached to cranium along whole width, maxillae movable only from stipes. [Cranium almost always oblong, epicranial halves fused along whole length, jointly rounded behind, occipital foramen ventral.] (Fig. 7D.) . . . . . Lamiinae

4(3) Distinct four-jointed legs (excluding coxa) present (trochanter may be strongly reduced and inconspicuous). Free movable cardo present (rather small in some Aseminae). [Epicranial halves in dorsal view usually separately rounded behind, cranium subquadrate to transverse.]

5(8) Metatentorium forming wide flat rigid bridge lying fully in same plane with hypostoma. Hypostomal plates large, anteriorly connected by very narrow gular bridge (usually distinctly narrower than metatentorial bridge), gula very shortly exposed or fully covered by postgular lobe (Figs 7A, 8A). Main antennal sensillum flat (Figs 20C, 22D), rarely roundly convex (Figs 15D, 20D), never conical. [Distinct pleural discs often present at least on abdominal segment 1.]

6(7) Basal half of pronotum (and less distinctly also some other body areas) ± roughly asperate (Fig. 15A). Labrum cordate, very long (Fig. 14E). [Epistomal, frontal and postcondylar carinae absent.] . . . . . Parandrinae

7(6) Body without coarse asperities. Labrum never as long as in *Parandra*. [Distinct epistomal, frontal and postcondylar carinae often present.] . . . . . Prioninae

8(5) Gula longer, exposed, metatentorial bridge very narrow medially, mostly only ligamentous (its width incomparable with medial gular length), at least medially slightly sunken under ventral cranial plane, but usually ± internal and poorly visible to invisible in ventral view (Figs 6E, 7C, 25D, E). Main antennal sensillum prominent, conical (Fig. 8D). [Never with distinct pleural discs.]

9(12) Praetarsus without seta. Frontal lines enter separately dorsal doubled cranial region far behind its anterior extremity (Fig. 7C). Epipleurum protuberant on abdominal segments 7 to 9. [Epicranial halves fused along whole length, cranium not, or very shallowly notched behind (Figs 29B, C). Lateral furrows of pronotum long and distinct (Figs 26C, 28A, 30D).]

10(11) Large postnotal fold present. [Epistomal margin projecting, or at least abruptly bulging, above clypeus. Urogomphi absent. Dorsal ampullae with one lateral impression on each side.] . . . . . Apatophyseinae

11(10) Postnotum non-developed. [Epistomal margin ± obliquely sloping and smoothly passing into clypeus, not projecting. Urogomphi present (may be absent in *Nothorhina* and in very young larvae of some other species). Dorsal ampullae with two lateral impressions on each side (Figs 11A, B, 26A, 32B) except for African *Pectoctenus* (Fig. 26B).] . . . . . Aseminae

12(9) Praetarsus bearing distinct seta (Fig. 25B), its absence on some leg is rare and aberrant. Frontal lines meeting (Fig. 6E), or almost meeting (Fig. 24A) each other at frontal base. Abdominal epipleurum protuberant at least on segments 6 to 9, usually on all except anal segment. [Lateral furrows rarely long and distinct. Epicranial halves very rarely (*Xylosteus* of Lepturinae) fused along whole length, cranium therefore almost always ± deeply notched behind.]

13(14) Dorsal ampullae with two broadly separate lateral impressions on each side (Fig. 25C). Prothoracic lateropraesternum largely microspiculate. [Lateral furrows distinct at least in hind half of pronotum.] . . . . . Necydalinae

14(13) Dorsal ampullae with one lateral impression (Fig. 9B), in any case never with two broadly separate impressions on each side. Lateropraesternum microspiculate at most along anterior margin. [Lateral furrows mostly rudimentary or absent.] . . . . . Lepturinae

Subfamily Parandrinae BLANCHARD, 1845

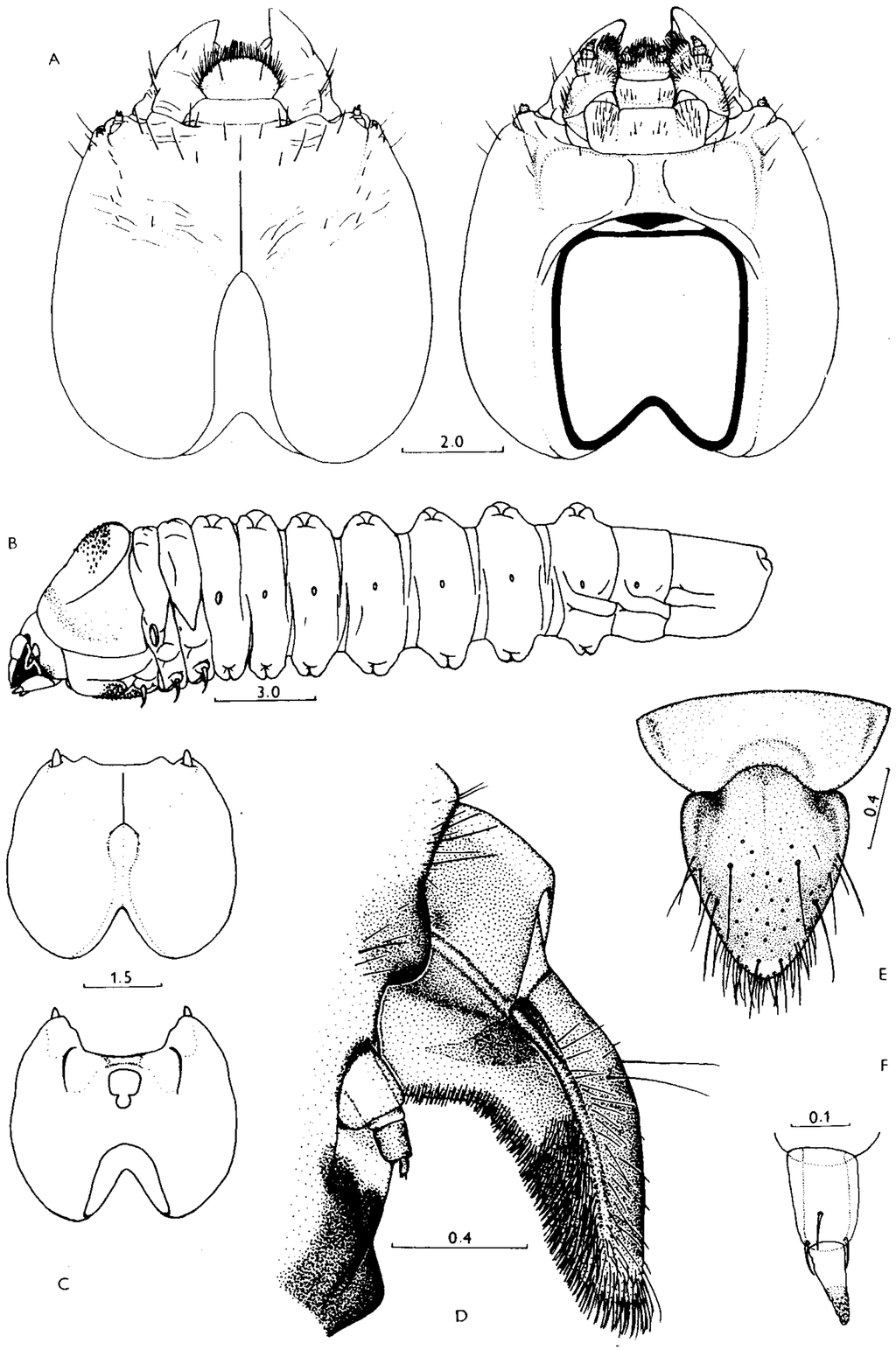
Larvae of one single genus available and known to me.

Genus *Parandra* LATREILLE, 1804

Type species: *Parandra laevis* LATREILLE, 1804 (monobasic)

Body white, elongate, slightly tapering posteriorly, cylindrical, non-depressed, with short thin setae. Numerous body areas covered with microscopic spines which often become larger (particularly on thorax), making certain areas coarsely asperate.

Head essentially of Prionine type; more than by half retracted. Cranium subquadrate (about 1.1–1.2), moderately depressed (about 1.7–1.9), much narrower than prothorax, sometimes slightly constricted about middle, widest behind middle; white or at most pale yellowish except mouthframe, at most feebly microgranulate anteriorly. Epicranium smooth, sides rounded, hind two-thirds glabrous, anterior one-third with short setae, dorsal longitudinal rows of setae present, moved far forward, not very conspicuous. Both epicranial halves broadly fused (Fig. 14C), diverging well before hind cranial margin which is thus distinctly notched. Frontal lines inconspicuous or indiscernible due to pale cranium, do not enter antennal openings, run below them, in some species reaching anterior cranial margin and broadly interrupting dark pigmentation of mouthframe, in others not reaching that margin, then mouthframe continuously pigmented. Hind extremities of frontal lines



not meeting each other, enter separately dorsal doubled cranial region - in other words, the latter region protrudes deeply into frontal region. Transfrontal line absent. Frons ± convex, pale, almost smooth (postcondylar carinae absent), glabrous behind, all setae shifted to anterior margin, some of them may be hardly distinguishable from true epistomal setae. These are six or more in number, rather distant from hind clypeal border. Separate epistoma absent, epistomal margin simple, roundly declivous towards clypeus, usually very pale except for very narrow dark band along sharply impressed clypeal border and large dark spots at mandibular articulations, seldom *(P. puncticeps)* epistomal margin distinctly sclerotized along whole width. Medial frontal line narrow, distinct, ± reaching epistomal margin. Clypeus filling entire space between mandibular articulations, convex, roundly tapering, usually emarginate and as if somewhat »excavated« anteriorly (Figs 14D, E), mostly with wide pigmented strips along sides, devoid of setae. Labrum extremely long (Fig. 14E), cordate, facing pronouncedly anterodorsad with apex pointed below (Fig. 14D); overall sclerotized and pigmented except for apex. Dorsal surface bearing many distinct sunken sensilla, two discal setae isolated, rarely accompanied by other small ones. Apical margin setose, also lateral edges fringed with rows of setae from above. Epipharynx with its anterior area almost perpendicular to the narrow abruptly raised posterior portion (Fig. 14D) due to anterodorsal position of the labrum. Tormae broad at base, tapering and curved backwards. Anterior epipharyngeal area bearing dense stout setae (in certain species some setae of peculiar shape - - with their ends flat, cut, chisel-like), two rows of setae reaching far behind to posterior extremities of tormae. Hind portion with anterior medial group of sensilla between posterior extremities of setal rows, the sensilla not arranged in a transverse row, without any sclerite behind them (but they themselves usually lie in a sclerotized area. Pleurostoma feebly raised, deeply sclerotized, dark brown to almost black in later instars, and often perpendicularly rugose at mandibular articulations. Subfossal process absent. Gena smooth or finely rugose, dark pigmentation usually about as wide as pleurostoma, rarely genal area not distinguished from epicranium. Stemmata usually absent, in some species the main stemmata present, then with four pigmented spots in vertical row under ± joined feebly convex cornea (Fig. 15E), dorsal stemmata faintly visible in *P. punctata.* Ventral stemma always absent. (For commentary upon presence of four main stemmata on one side see the general morphological chapter of Prioninae.) Hypostomal sclerites large, flat, triangular, glabrous, smooth or often transversely rugose. Anterior margin narrowly pigmented, hypostomal lines distinct, narrow, diverging basally, then gradually curved and

Plate 14: A — *Dorcasomus gigas* (Africa), head, dorsal (left) and ventral (right) views. B — *Parandra brunnea,* later instar larva, lateral view. (Setae not figured.) C — *P. brunnea,* outline of cranium, dorsal (upper) and ventral (lower) views. D — *P. caspia,* mature, part of mouthframe, antenna, clypeus, labrum and epipharynx (right mandible removed), lateral view from right side. E — *P. brunnea,* later instar, clypeus and labrum, anterodorsal view. F — *P. brunnea,* apical part of mesothoracic right leg (from DUFFY, 1953).

converging, vanishing about at level of hind margin of small anterior portion of occipital foramen. Gular bridge extremely narrow (Fig. 14C), gula very shortly exposed (Fig. 15A), with narrow dark anterior band continuous with that of hypostoma. Metatentorial bridge very broad, rigid, lying in the same plane as the hypostomal plates, thus dividing occipital foramen into a small anterior and a large posterior portions (Fig. 14C). Metatentorial pits absent.

Antennae (Figs 15D, E) long, three-segmented, pointed obliquely ventrad. Antennal ring almost not raised, narrowly continuously pigmented, not interrupted by frontal line. Connecting membrane large, prominent, antennae deeply retractile. Segments cylindrical, pigmented (segment 1 only in its apical part), segment 3 minute, slender. Main sensillum large, flat, in some species roundly convex (Fig. 15D), never conical. Mandibular type II (Fig. 16A) very well developed, mandible short, robust. Apex strongly produced, very sharp, dorsal angle short, magnificent type-II keel with large dorsal and inner striated plates present, dorsal striated plate covered by the very long labrum when mandibles are closed. Apical portion with two or three inner keels, lateral face ± smooth, mostly shining. Border zone slightly impressed, striate or microsculptured. Outer face of basal portion rough, bearing greater number of setae, inner face ± smooth. Labiomaxillary complex non-depressed, relatively gracile in comparison with typical Prioninae (Fig. 15A), attachment to cranium slightly wider than gula. Basal components separate, submentum medially longitudinally raised, connecting lobe with diffuse pigmented spot, cardo large, free, movable, seta absent. Distal maxilla rather slender, stipes with basal pigmented band broad but sometimes incomplete. Palpiger pigmented, separate basal spot and laterodorsal process absent, palps three-segmented, segments subequal in length. Mala narrow, subcylindrical (inner face not keeled), shorter than palp, pigmented except for apex, bearing numerous stout setae. Distal labium short, mentum broad (but not distinctly broadened anteriorly as in most Prioninae), with uninterrupted basal pigmented band. Pigmentation of labial palpigers fused medially, palps two-segmented, lateroventral in regard to ligula, the latter is broad, rounded, with stout reddish apical and dorsal setae, microtrichia restricted and inconspicuous.

Prothorax broadest of body segments, most of its regions in later instar larvae finely sclerotized, yellowish. Pronotum large, inclined forward (Fig. 14B), bearing many scattered short setae. Anterior transverse band narrow, broadened on alar lobes, anterior margin with one small notch on pronotum and one on alar lobe on each side; in some species pigmentation very inconspicuous. Posterior half of pronotum broadly raised, ± coarsely asperate (covered with ± large sclerotized grains

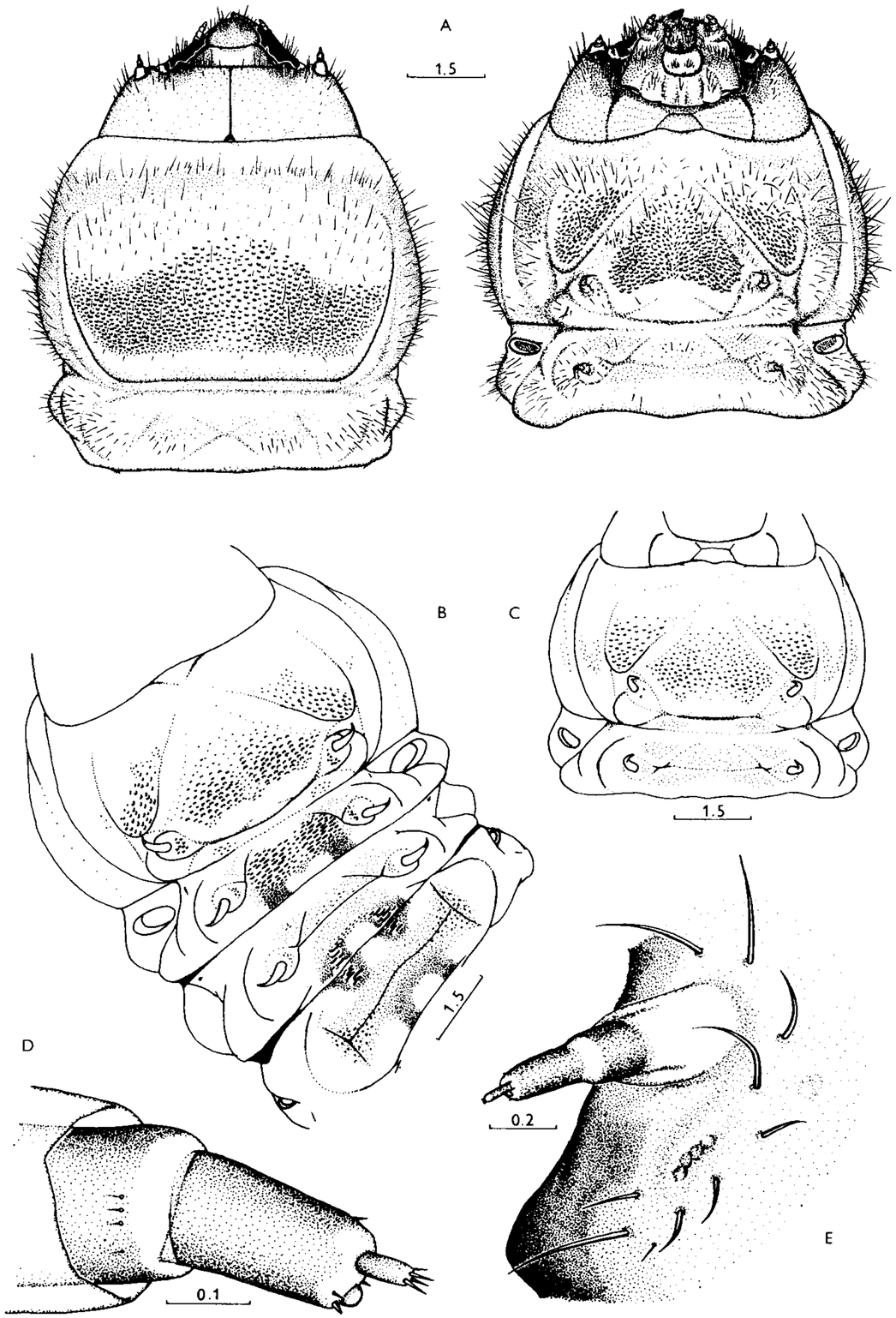


Plate 15: A — *Parandra caspia,* mature, head, pro- and mesothorax, dorsal (left) and ventral (right) views. B — *P. glabra,* later instar, diagrammatic illustration of thorax and first abdominal segment in ventral view, showing distribution of asperities. C — *P. brunnea,* mature, pro- and mesothorax, diagrammatic, ventral view. D — *P. brunnea,* mature, right antenna, lateral view. E — *P. punctata,* later instar, left pleurostoma, gena and antenna, anterolateral view. (Note four main stemmata.)

with sharp raised hind edges). Lateral furrows distinct, not reaching anterior margin, not interrupting anterior pigmented band. Alar lobes large, triangular, occasionally with inconspicuous microscopic spines. Epipleurum similar to Prioninae (broad in front instead of tapering), often with spines. Prothoracic venter rather modified, similar to certain Prioninae. Mediopraesternum expanded backwards, thus reducing coxosternum and sternellar fold - the former much reduced, both halves very broadly separate, their medial extremities pointed obliquely backwards; the latter extremely short, poorly separated from (Figs 15B, C) or partly medially fused with (Fig. 15A) the mesothoracic sternum (often folded between mediopraesternum and mesothoracic sternum and invisible externally). Anterior border of mediopraesternum obscure, and a new line (out of the original one) developed (Fig. 15A) - a situation analogous to most Lamiinae. Episternum defined, small, triangular, unsclerotized. Postgular lobe distinct, moderately large (Figs 15A, C), in some species finely sclerotized (it is possible that the postgular lobe is at least partly homologous with posterior gular region of some other subfamilies). Both divisions of praesternum coarsely asperate, sclerotized spines often present also on coxosternum and sternellar fold.

Both meso- and metanotum divided by conspicuous X-shaped lines, covered with mostly fine microscopic spines. Postnotum non-developed; in some species a very narrow separate transverse intersegmental band present behind pronotum. Scutum I feebly defined on mesothorax, relatively distinct on metathorax. Alar lobes not protuberant. Mesothoracic spiracle at the border of epipleurum and alar lobe, almost not protruding into prothorax, narrowly elliptical, sclerotized, marginal chambers of varying number, size and position (Figs 16E, F), sometimes almost wanting. Praesternum small, triangular. Pleurum large, broadly separating coxae from epipleurum, undivided. Sterna non-granulate, bearing spines (occasionally partly modified into characteristic larger asperities - Fig. 15B). Transsternal line often obscure about middle, in mesosternum may be even absent. Basisternum divided by a pair of distinct deep oblique impressions. Coxae defined, small, with a few spines on inner face.

Distal leg (Fig. 14F) moderately long, four-segmented, bearing very short sparse setae. Trochanter minute, annular, without conspicuous pigmented ring. Other segments subequal in length, or femur shorter. Tibiotarsus much more slender than femur. Practarsus slender, straight, conical, not compressed, devoid of setae, microasperate, with at most its tip pigmented.

Abdomen with rather sharply protuberant non-granulate ampullae on segments 1 to 7. Ampullae ± deeply impressed medially, covered with spines, gradually narrowing from 1 to 6, ampulla 7 (esp. the ventral one) smaller. Dorsal ampullae (Fig. 16D) with praescuto-scutal line simple, scuto-scutellar line incomplete, one longitudinal impression on each side. Parascutum in some species bearing spines (apart from those belonging to dorsal ampulla) which may even spread on spiracular area. Spiracles oval, ferrugineous, first abdominal spiracle much larger than others. Marginal chambers of varying size and number. Very narrow protuberant epipleurum

present on segments 7 to 9 (Fig. 14B), on anterior six segments ± fused with the neighbouring areas. Pleural tubercles ill-defined, pleural discs absent. Ventral ampullae with transsternal line and lateral longitudinal impressions distinct. Pleural lobe at most feebly separate. Segments 8 and 9 lacking spines, ninth segment long (longer than segment 8), broadly rounded posteriorly (Fig. 14B), similar to certain Prioninae (cf. Fig. 22E). Caudal armature absent. Anal segment fused with segment 9, anus triradiate, slightly posterodorsal, anal papillae distinct, bearing short setae.

Classification: The genus *Parandra* is undoubtedly close to Prioninae. Its position has been briefly discussed in the chapter dealing with higher classification.

Distribution: Mainly tropical and subtropical group. In Holarctic Region very few species, only offshoots of southern fauna, the North American *P. brunnea* being the only one truly »temperate« species.

Bionomics: Larvae infest mostly decaying moist wood, often of living trees (hollows etc.), preferably deciduous. They are often present in great number. Pupation in the wood. Adults lead very hidden mode of life. CRAIGHEAD (1950, cited after LINSLEY, 1962a) writes about *P. brunnea*: »This larva bores gregariously in the dead, but moist, heartwood of practically all hardwood and many coniferous trees in contact with the ground and also in cavities in living trees throughout the United States east of the Rocky Mountains. ... A small wound near the base of a living tree may offer a place of entrance for the young larvae, which will continue to feed in the heartwood until nothing remains but a shell of sapwood. Under certain circumstances the adults do not emerge but mate and lay eggs in the same cavity in which they are working. Often the wound where they gained entrance heals over and shows no sign of their presence.« These peculiar habits are perhaps responsible for the peculiarities of adult morphology. *P. brunnea* is considered very destructive in North America, particularly to shade trees and structural timber in contact with ground.

In Europe and Soviet Union, one indigenous and one introduced species:

1(2) Body setae sparser (Fig. 16C). Spiracles with marginal chambers larger (Fig. 16F). At least some of first seven abdominal segments with spines on parascuta (may be fully absent from very young larvae). North America, introduced and established in Europe, German Democratic Republic (sg. *Neandra* LAMEERE, 1912) . . . . . *brunnea*

2(1) Body with setae denser (Fig. 16B). Spiracles with small and in average more numerous marginal chambers (Fig. 16E). Abdominal parascuta without spines except for those on ampullae. South coast of Caspian Sea (sg. *Archandra* LAMEERE, 1912) . . . . . *caspia*

Parandra (Neandra) brunnea (F., 1798)

Pronotum and propraesternum very coarsely asperate. Microscopic spines on pterothorax and abdomen scarce, uniform and distinct. Setae sparse, reddish brown. Cranium rather distinctly constricted about middle. Pigmentation of mouthframe broadly interrupted by frontal lines. Six strong epistomal setae, supplementary setae absent or few and miniature. Anterior extremity of medial frontal line diffuse in mature larvae. Gena pigmented, ferrugineous. Stemmata absent. Antennal segment

2 longer than broad, only in very young larvae its length almost equal to width. Main antennal sensillum somewhat prominent, roundly convex (Fig. 15D). Mandible with two inner keels reaching apex, border zone not striate, microgranulate. Mala rather long and slender. Pigmented band of prothorax inconspicuous, epipleurum with spines, sternellar fold narrow yet defined posteriorly (Fig. 15C), bearing a few lateral spines. Intersegmental zone behind pronotum very narrow. Mesothoracic spiracle with relatively large marginal chambers (Fig. 16F), transsternal line of both meso- and metanotum obscure but present. Lengths of distal three leg segments subequal, praetarsus with apex pigmented. Parascuta of abdominal segments 1 to 7 (or at least of some of them) bearing a few spines (beside those on ampullae). Abdominal spiracles with rather large marginal chambers. Length up to 40 mm.

Bionomics: Polyphagous, but deciduous trees apparently preferred. Habits as described above. Several-year life-cycle.

Material: 1951 USA, Ohio, Columbus, many larvae from *Malus,* coll. Ohio State University, Columbus; 1982 GDR, Dresden, one larva from *Tilia,* coll. M. Sláma.

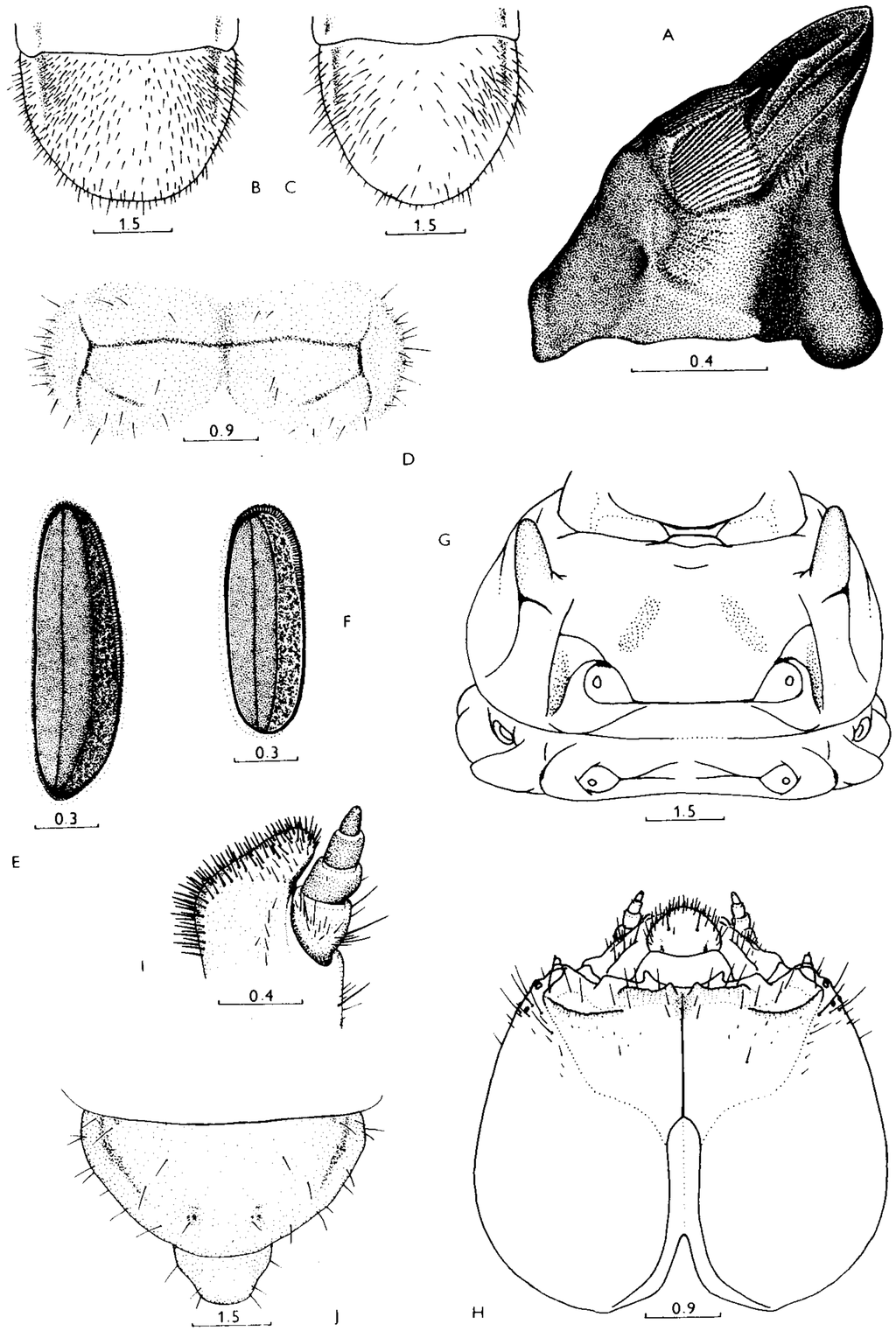
Parandra (Archandra) caspia MÉNÉTRIÈS, 1832

Similar to *P. brunnea,* main differences as follows: Setae much more dense. More than six epistomal setae in later instar larvae. Medial frontal line distinct along whole length, somewhat diffuse at most immediately behind posterior clypeal margin. Antennal segment 2 about as long as broad, main sensillum flat. Mandibles with border zone striate. Mala shorter, more robust. Prothorax of mature larvae with pigmented band relatively distinct, epipleurum with or without spines, sternellar fold extremely reduced and practically fused medially with mesosternum, without lateral spines. Intersegmental zone behind pronotum broader. Mesothoracic spiracle with more numerous extremely small marginal chambers. Meso- and metasternum with transsternal lines distinct. Abdominal parascuta devoid of spines (except on ampullae), spiracles with small chambers. Length up to 42 mm.

Bionomics: Polyphagous on deciduous trees. Larvae in dead decaying hardwoods of greater diameter. Pupation in spring/summer (in Iran, pupae found June 28). At least three-year development judging from the larvae collected together with pupae.

Material: 28. 6. 1977 Iran bor., Punel, 4/I, *Carpinus,* collected by expedition of Prague National Museum, coll. Nat. Mus. and S; 9. 6. 1979 SU, Azerbaidzhan SSR, Avrora, 3/I, *Quercus,* lgt. D, coll. S.

Plate 16: A — *Parandra caspia,* later instar, left mandible, medial view. B — *P. caspia,* later instar, ninth abdominal segment, ventral view. C — *P. brunnea,* later instar, dtto. D — *P. caspia,* mature, first dorsal ambulatory ampulla. E — *P. caspia,* mature, left mesothoracic spiracle. F — *P. brunnea,* mature, dtto. G — *Eudianodes swanzyi* (Africa), pro- and mesothorax, diagrammatic, ventral view. H — *Tragosoma depsarium,* half-grown, head, dorsal view. I — *T. depsarium,* half-grown, apical part of right maxilla, dorsal view. J — *T. depsarium,* later instar, abdominal segments 9 and 10, dorsal view.



(For distribution of both species see the key.)

Additional species available: *Parandra punctata* (April 1957, British Guayana, Bartica dist.), *P. glabra* (December 1947, Brazil, ex *Araucaria brasiliensis,* F. Plaumann lgt.), *Parandra* sp. close to *glabra* (9. 7. 1967, Dominica), *Parandra* sp. (4. 11. 1932, Sao Thomé I.), *Parandra* sp. with no data - all from collection of the British Museum (N. H.), London; *Parandra puncticeps* (25. 6. 1932 Hawaii, Kumuweia Kauai, ex *Piptur albidne*), *Parandra* sp. probably *marginicollis* (4. 2. 1969, USA, Calif., L. A. Co., ex *Eucalyptus,* lgt. Williams and Okumura) - both from collection of the U. S. National Museum, Washington.

Subfamily Prioninae LATREILLE, 1804

General morphology

Body white or yellowish, usually large, elongate to rather robust, cylindrical, non-depressed, with short thin setae.

Head very deeply retracted. Cranium subquadrate or very slightly transverse (1.0–1.3), moderately depressed (1.7–2.0), widest behind middle or almost parallel-sided, much narrower than prothorax, the retracted portion ± unpigmented and glabrous. Dorsal rows of four small setae on each side absent, or at least incomplete. Epicranial halves broadly fused and separately rounded behind, cranium shallowly emarginate to deeply notched posteriorly. Frontal lines from distinct to almost indiscernible in their posterior section, mostly S-curved, posterior extremities enter separately the dorsal doubled cranial region, anterior extremities may or may not reach cranial margin; entering antennal openings, touching them from below, or ending blindly. In many species there is a short blind supplementary cleavage line branching off from the anterior extremity of the frontal line, running down between pleurostoma and gena, so that the mouthframe remains intact during ecdysis. In some species with the cranium heavily sclerotized anteriorly, long anterior sections of the frontal lines become non-functional and the cranial cuticle breaks behind the anterior sclerotized portion which thus remains intact as a whole in the exuvia (Fig. 18D). Transfrontal line absent. Frons from relatively short to very long (Fig. 23B), mostly ± distinctly broadly transversely impressed at base. Usually 4–6 pairs of stouter anterior frontal setae, in later instar larvae mostly accompanied by variable number of other (usually smaller) ones. Separate epistoma present, ± projecting over clypeus (Figs 7A, 8A), dentate and/or carinate, rarely absent (Fig. 23B). Anterior frontal margin above the epistoma carinate and/or dentate as well, rarely this frontal carina rudimentary or absent. Postcondylar carinae mostly present. The latter three structures exert, however, remarkable geographical, individual and particularly growth variability. Epistomal setae lying between epistomal and frontal carinae; they are usually six in number, occasionally more, in some species of *Prionus,* however, the medial pair tends to disappear. Moreover, in later instar larvae with heavily sclerotized mouthframe the epistomal setae may be rather small,

some of them occasionally absent, or very often broken. Medial frontal line distinct, narrow, ± reaching anterior frontal margin. Clypeus filling the entire space between dorsal mandibular articulations, trapezoidal, without setae, often distinctly impressed anteriorly at middle. Labrum from about as long as broad to strongly transverse, of varying shape, never elongate as in *Parandra.* Epipharynx with numerous setae reaching far backward, occasionally along the whole posterior raised portion (Fig. 19C), microtrichia at most restricted and small. Tormae running obliquely backwards, mostly long, often broken into two parts. Pleurostoma ± raised, always deeply sclerotized, often with a distinct longitudinal keel. Subfossal process mostly large, conical, rarely absent. Gena sclerotized and pigmented to varying extent, often finely rugose, almost always protuberant behind the main stemmata making them facing forward (this protuberance mostly preserved even if the stemmata are absent - - *Prionus*). Stemmata from six pairs to absent, main stemmata usually three on each side, rarely fusing. In some individuals of certain genera (*Megopis, Ergates,* undoubtedly possible also in others), four main stemmata have been found on one or even both sides (cf. *Parandra*). The fourth main stemma occurs very rarely yet so frequently that it can be hardly interpreted as a random abnormality. If the two dorsal and one ventral stemmata are present, then there are seven stemmata on one side in such individuals (Fig. 18B), which number is characteristic for some other larvae of Holometabola, although I know no beetle larvae with regular seven pairs of stemmata. Thus, a possibility cannot be ignored of the fourth main stemma being an atavism, corresponding with the seventh stemma of certain holometabolous larvae. In addition to Parandrinae and Prioninae, I have seen one larva of *Derolus mauritanicus* (Cerambycinae, Cerambycini) having four main stemmata on one side. Dorsal and ventral stemmata mostly less distinct than the main ones, often inconstant or somewhat variable in position. Hypostomal lines distinct, slightly S-curved to straight, abruptly converging posteriorly, mostly reaching postoccipital line (Fig. 7A). Hypostomal sclerites large, triangular, glabrous or bearing at most extremely minute setae. As in *Parandra,* the two hypostomal sclerites are anteriorly bridged by very short gula developed as a very narrow transom. The gula may be shortly exposed and visible externally, or ± completely covered by the postgular lobe; the latter may be somewhat sclerotized. Metatentorial bridge broad, rigid, usually distinctly broader than the gular bridge, lying entirely in the plane of hypostoma, the occipital foramen seems to be divided (Fig. 7A). Metatentorial pits absent.

Antennae moderately to very long, two- or three-segmented (the third segment present or absent, first two segments never fusing with each other), rather deeply retractile. Antennal ring often projecting over dorsomedial region of the connecting membrane as a large antennal shell (e.g. Fig. 18D). Segments always distinctly pigmented, the first segment may bear in some species a few shorter or longer dorsal subapical setae. Main antennal sensillum rather large (relatively diminishing in the successive instars), subcircular to oval in apical view, flat (remarkably protuberant in some *Prionus*-species, Fig. 20D, but never conical). Mandibles short, robust,

with prominent apex and sometimes rather reduced dorsal angle. Mandible generally of the type II, but the type II-keel reaching apex (Fig. 17D). In many species the anterior section of the keel is continuous not with its posterior section but with one of the ridges of the dorsal striated plate (Fig. 23A). In other species this arrangement is not distinct, and the apex and dorsal angle are connected by a continuous edge. The striated plates may be modified (e.g. with only a few coarse ridges, Fig. 23A), or much reduced. Finally, the mandible may have one single dorsal ridge on apical part (*Callipogon* - Fig. 21G, *Prionus* - Figs 20A, E, F) corresponding to the lateral edge of the striated plate, or even this ridge may be indistinct. Such mandible resembles mandibular type I, their cutting edges are, however, non-homologous, that of the type II corresponding to the dorsal ridge of the mandible of Prioninae. Mostly three inner keels present. Basal mandibular part always bearing greater number of short lateral setae, in some species the molar part with a group of short decumbent setae on the dorsal surface near inner margin (Fig. 23A). Labiomaxillary complex robust, bearing comparatively numerous short setae, those of ligula and mala mostly remarkably stronger. Attachment of the labiomaxillary complex to the anterior cranial margin much wider than the gula. The labiomaxillary complex has a ± distinct narrow separate transverse basal area (Figs 17C, 19B, 20A) which is not developed in other groups (including Parandrinae and *Anoeme*). Connecting lobe large, convex, mostly bearing numerous setae. Cardo large, free, movable, without distinct lateral seta, at most with one or a few extremely minute setae on posterior face. Stipes with basal pigmented band laterally absent or at least strongly reduced. Palpiger pigmented at base, lateral face rounded, or sometimes remarkably flattened, the laterodorsal process rarely present. Maxillary palp three-segmented, exceeding the mala, segment 1 without process. Mala short, mostly relatively broad, triangular and with sharp carinate inner edge, more rarely narrow and cylindrical but even then not making an impression in ventral view that it grows out exclusively from the palpiger. Mala always with oblique pigmented band. Mentum may be almost fused with submentum; the former of rather characteristic shape, ± trapezoidal, broadest anteriorly, with large prominent rounded setose anterior angles. Labial palpigers poorly separate from praementum, their pigmentation often fused into an uninterrupted band. Laterally this band extends dorsad along both sides of labium, and the dorsal labial portion is often notched between dorsal ends of the band (Fig. 18C, cf. with 18F), thus separating an anterior and a posterior (supposedly hypopharyngeal) dorsal labial portions. The notch is therefore called hypopharyngeal in the following descriptions. Labial palps short, almost lateral in regard to ligula, the latter broad, rounded, covered with rather dense stout setae reaching backwards at least to the hypopharyngeal notch *(Callipogon),* but the hind (hypopharyngeal) portion usually also bearing setae. Ligula sometimes with narrow basal lateroventral pigmented spots.

Pronotum usually ± rugose, with greater number of short setae, with or without a medial impressed line. Anterior pigmented band very distinct to almost absent,

often non-homogeneous (the pigment divided into smaller separate spots), with two pairs of anterior notches (one on alar lobes, one on pronotum). Lateral furrows distinct but not interrupting the pigmented band. Sublateral impressions mostly ± distinct (Fig. 10A), broad, shallow, transverse or oblique. Alar lobes very large, Epipleural fold broad in front, not tapering, but the anterior section of its ventral border line apparently secondary (a lateral portion of lateropraesternum fused with epipleurum). Posterodorsal epipleural angle often separate, sometimes fused with the alar lobe. In some groups (*Eudianodes* - Fig. 16G, *Eurypoda* - KOJIMA, NAKAMURA et HAMADA, 1966) the epipleurum anteriorly produced into a very large fleshy process. Pleural sulcus distinct, straight to S-curved, projecting inwards as a small apodeme (only few species examined for this latter character). Episternum sharply defined, ± sclerotized, often pigmented, sometimes longitudinally protuberant, in some species with deep broad lateral impression. Mediopraesternum from sharply defined to fusing anteriorly with the lateropraesternum. Coxosternal halves from large, transverse, almost meeting each other medially, to very small and broadly separated by the expanded mediopraesternum (Fig. 23C) which is the case in *Parandra.* Sternellar fold separate, never fusing with mesothoracic sternum.

Meso- and metanotum with praescuto-scutal and scuto-scutellar lines ± distinct, separate or fused and X-shaped. Mesonotum may be unmodified (Fig. 23C), or the postnotal fold may be developed (Fig. 18A, rather poorly in *Rhesus* and some related Australasian genera, Fig. 22B), but never as distinct and as closely adjacent to prothorax as in Apatophyseinae and Cerambycinae. Scutum I defined or obscure, more distinct on metathorax. Alar lobes non-protuberant, deeply wedged into the epipleurum. Mesothoracic spiracle lies entirely in anterior epipleural region, protruding slightly into prothorax; oval, of varying relative size, marginal chambers small, in some species very numerous, occasionally absent. Rudimentary metathoracic spiracle distinct to indiscernible. Praesternum well defined. Pleurum entire (pleural sulcus absent), large, broadly separating coxae from epipleurum. Coxae small, sharply defined. Transsternal lines present, at most less conspicuous about middle. Medio- and laterobasisterna not separated from each other, but a pair of similar more medial oblique lines mostly present (Fig. 10A).

Distal legs short to very short, at most slightly longer than maxillary palps, four-segmented, but trochanter very short, annular or unequal (lateral portion much more reduced), in some species very much reduced, nearly absent, basal sclerotized ring at most incomplete, crescent-shaped. Femur and tibiotarsus with lateral face often pigmented, inner face mostly bearing numerous setae contrasting with relative scarcity of body setae (the legs, being of no locomotory use at all in the present subfamily, perhaps serve as sensory appendages). Praetarsus conical, non-flattened, not curved, apical part microasperate, may be sclerotized. In some species (notably in *Ergates*), praetarsus may bear one or even several minute setae, but their presence, number and position are inconstant.

Abdomen: Dorsal and ventral ambulatory ampullae seven with no exception

known to me, the seventh ampulla at most slightly reduced. Ampullae smooth, or ± rugose, very rarely (e.g. *Eudianodes*) finely granulate, having rather uniform pattern (dorsal ampulla with two main transverse simple lines connected by one lateral impression on each side, ventral ampulla with one complete transverse line, one pair of lateral impressions and mostly with relatively distinct second posterior incomplete transverse line). Pleural lobes well defined at least on a few anterior segments, their border furrows ± moved on the protuberant ampulla (i.e. the coxal lobe rather small). Ampullae never deeply medially impressed or even bilobed. Spiracles similar to the mesothoracic one, always much smaller, those of segment 1 at least slightly larger than others, spiracles 7 and 8 may be somewhat larger, too. Epipleurum of segments 1 to 6 non-protuberant, but its upper and lower boundaries are not entirely lost; pleural tubercles of those segments obscure, more or less distinct radially striate pleural discs present at least on the first segment, in some groups on all six segments, then the first disc largest. Six pairs of extremely large and distinct discs found in the genus *Prionus*. Segments 7 and 8 with the epipleural fold abruptly protuberant (less so in unnaturally extended larvae), pleural tubercles large, distinct, pleural discs absent. Segment 9 large, as long as, or often longer than segment 8 (Figs 17A, 22E), epipleurum at least anteriorly protuberant, no tubercles or discs, caudal armature absent (for possible vestigial urogomphi see description of the genus *Tragosoma*). Anal tube short, separate or often ± fusing with the ninth segment, terminal or posterodorsal, never ventral. Anus triradiate, anal papillae distinct.

Classification: As far as the larvae are known, the group is relatively coherent, with a partial exception of the genus *Anoeme* (see the chapter on problematic larval forms). In fact the genus Anoeme differs as much from Prioninae as the genus *Parandra*. As the Palaearctic Prioninae are rather few, and often only marginal representatives of main stocks with other distributional centers, I have not tried to include tribal classification (nevertheless, as far as the usual tribal classification concerns, I would like to point out that it is undoubtedly incorrect to classify the genera *Ergates* and *Callipogon* in the same tribe, whatever its name may be). The generic descriptions in this subfamily must be often understood as provisional, as they are based solely on the available Palaearctic material, although many Prioninae larvae have been already accumulated in various collections throughout the world (the reasons for such approach have been discussed in »Material and methods«).

Distribution: Prioninae are distributed throughout the world, most abundant in warm climatic zones, in temperate and esp. cold regions are scarce.

Habits: Larvae live predominantly in dead and mostly decaying moist wood where also pupation takes place. Rarely (known in North American *Derancistrus taslei*) the larva feeds in »dry, dead, seasoned tops of various hardwoods« (CRAIGHEAD, 1923). Larvae of *Prionus* work mostly in roots (often in dead or dying roots of living trees), and, as far as known, pupate mostly in soil, in a cocoon constructed from wood and/or soil particles cemented together by larval secretion. Some larvae of *Prionus* came to feeding on roots of herbaceous plants and live all the time freely in the soil (also other *Prionus*-larvae are known to be capable of tunneling through

the soil from one root to another.) In Palaearctic species the development period seems to be always at least two or three years. Adults are mostly crepuscular or nocturnal, brownish or black, rarely brightly colored (some tropical groups). The subfamily is characteristic by total absence of very small forms.

Key to genera of Prioninae

1(2) Anterior frontal margin almost unpigmented except for large dark spots at dorsal mandibular articulations. Postcondylar, frontal and epistomal carinae in younger larvae absent, in later instar and mature larvae former two carinae present, vestigial (Fig. 23B). Prothoracic epipleurum distinctly divided by a transverse line. Postnotal fold non-developed (Fig. 23C) . . . . . *Macrotoma,* sg. *Prinobius*

2(1) Anterior frontal margin ± broadly sclerotized. Postcondylar, epistomal and frontal carinae present. Prothoracic epipleurum without distinct transverse line. Postnotal fold developed.

3(12) At least main stemmata present. Posterior pleural discs small, indistinct or nearly absent.

4(7) Third antennal segment completely absent, frontal carina at most with one pair of indistinct medial teeth (Figs 21G, 22C, D). Coxosternal halves small, broadly separated by expanded mediopraesternum (about as in *Macrotoma,* Fig. 23C).

5(6) Frons short, its medial length smaller than that of dorsal doubled cranial region (Fig. 21G). Epipharyngeal setae not reaching behind along posterior raised portion. Gula shortly exposed. Mala narrow, cylindrical, inner side not carinate (Fig. 22A). Dorsal labial portion with no setae behind hypopharyngeal notch, latter moved strongly forward, anterior portion very short . . . . . *Callipogon,* sg. *Eoxenus*

6(5) Frons very long (Fig. 22C). Epipharyngeal setae reaching behind along posterior raised portion. Gula completely covered by postgular lobe. Mala broader, inner face carinate. Hypopharyngeal notch situated more posteriorly, hypopharyngeal labial portion bearing setae . . . . . *Rhesus*

7(4) Antennae three-segmented (segment 3 much reduced in *Ergates,* Fig. 17G, in mature larvae may be almost incorporated in apical membrane of segment 2, but then frontal carina with two pairs of large teeth, Figs 18A, D). Coxosternal halves large, transverse, approaching or almost meeting each other.

8(11) Cranium deeply notched behind (Figs 16H, 17C). Gula shortly exposed.

9(10) Posterior cranial notch broad (Fig. 17C). Third antennal segment extremely reduced, knob-shaped (Fig. 17G). Palpiger process often present . . . . . *Ergates*

10(9) Posterior cranial notch narrow (Fig. 16H). Third antennal segment cylindrical, about as long as broad. Palpiger process absent. . . . . *Tragosoma*

11(8) Cranium hardly emarginate posteriorly (Fig. 19A). Gula covered by postgular lobe . . . . . *Megopis,* sg. *Aegosoma*

12(3) Stemmata absent. Six pairs of very large, distinct, sharply delimited pleural discs present (Fig. 21F) . . . . . *Prionus* (incl. *Dorysthenes*)

Genus *Tragosoma* SERVILLE, 1832

Type species: *Prionus depsarius* F., 1787 = *Cerambyx depsarius* L., 1767 (monobasic)

Body (Fig. 17A) short, robust, with reddish setae.

Cranium (Fig. 16H) subquadrate (1.1–1.2), moderately depressed (about 1.9), widest behind middle, almost not microgranulate, shining, anterior half pale yellow-

ish, posterior half unpigmented. Mouthframe heavily sclerotized. Epicranium with sides gently roundly convex, anterior setae sparse. Cranium deeply and rather narrowly notched posteriorly. Frontal lines narrow, not very distinct, slightly S-curved, touching antennal openings from below (but not entering them), reaching anterior cranial margin. Frons deeply impressed at base, relatively smooth, its medial length slightly to very distinctly greater that that of dorsal duplicated region. Mostly five or six pairs of anterior frontal setae. Postcondylar carina long, distinct, with dorsal face striate. Frontal carina well developed, rather broadly interrupted in middle, coarsely sculptured, with one ± distinct medial pair of teeth and often one or two short blunt rounded lateral teeth on each side. Only lateral portions of epistomal carina projecting distinctly over clypeus, there with one pair of prominent, rather slender processes (may be almost absent in young larvae). Six epistomal setae. Clypeus narrow, slightly convex, roundly tapering, basal half sometimes yellowish. Labrum about as long as wide, somewhat cordate, entirely sclerotized and pigmented except for apical margin, bearing unusually sparse stout setae along apical and lateral margins, dorsal face with some conspicuous sunken sensilla and two stout discal setae, other discal setae at most very small. Epipharynx almost unsclerotized, setae reaching to anterior one-third of hind raised portion. Tormae oblique, not connected with longitudinal sclerotized bands running along sides o- hind portion. Pleurostoma dark ferrugineous, with low blunt vertical carina, subfossal process distinct, conical. Gena relatively smooth, moderately broadly pigmenf ted, at most slightly wider than pleurostoma, then becoming gradually paler. All six pairs of stemmata mostly well discernible. Main stemmata three on each side (the fourth main stemma in the available material present at most as an indistinct paler spot), distinct, convex, with conspicuous pigment spots. Gena (particularly in young larvae) not much protuberant, main stemmata facing somewhat to sides. Dorsa stemmata two, slightly smaller, feebly convex, widely separate from each other, their position rather variable. Ventral stemma often rather inconspicuous, but usually visible. Hypostomal lines distinct, reaching postoccipital line, their anterior thirds pigmented. Gula shortly exposed, much narrower than one hypostomal sclerite, postgular lobe finely sclerotized. Metatentorial bridge broad, more than twice as broad as gular bridge (i.e. more than twice broader than »gular length« - - longitudinal dimension of the gular transom).

Antennae short, three-segmented. Projecting antennal shell well developed, often striate. Connecting membrane not projecting very far from antennal opening. Segments cylindrical, segment 1 with only very short setae, segment 2 at most slightly longer than broad, in young larvae may be somewhat transverse, main sensillum flat, subcircular, third segment about as long as broad. Mandible short, robust, outer face with coarsely striate border zone. Dorsal angle well developed, three inner keels present, apex and dorsal angle connected by simple continuous cutting edge, small inner and large dorsal finely striated plates present. Outer face of basal portion densely rugose, bearing numerous setae, remaining surface smooth, shining

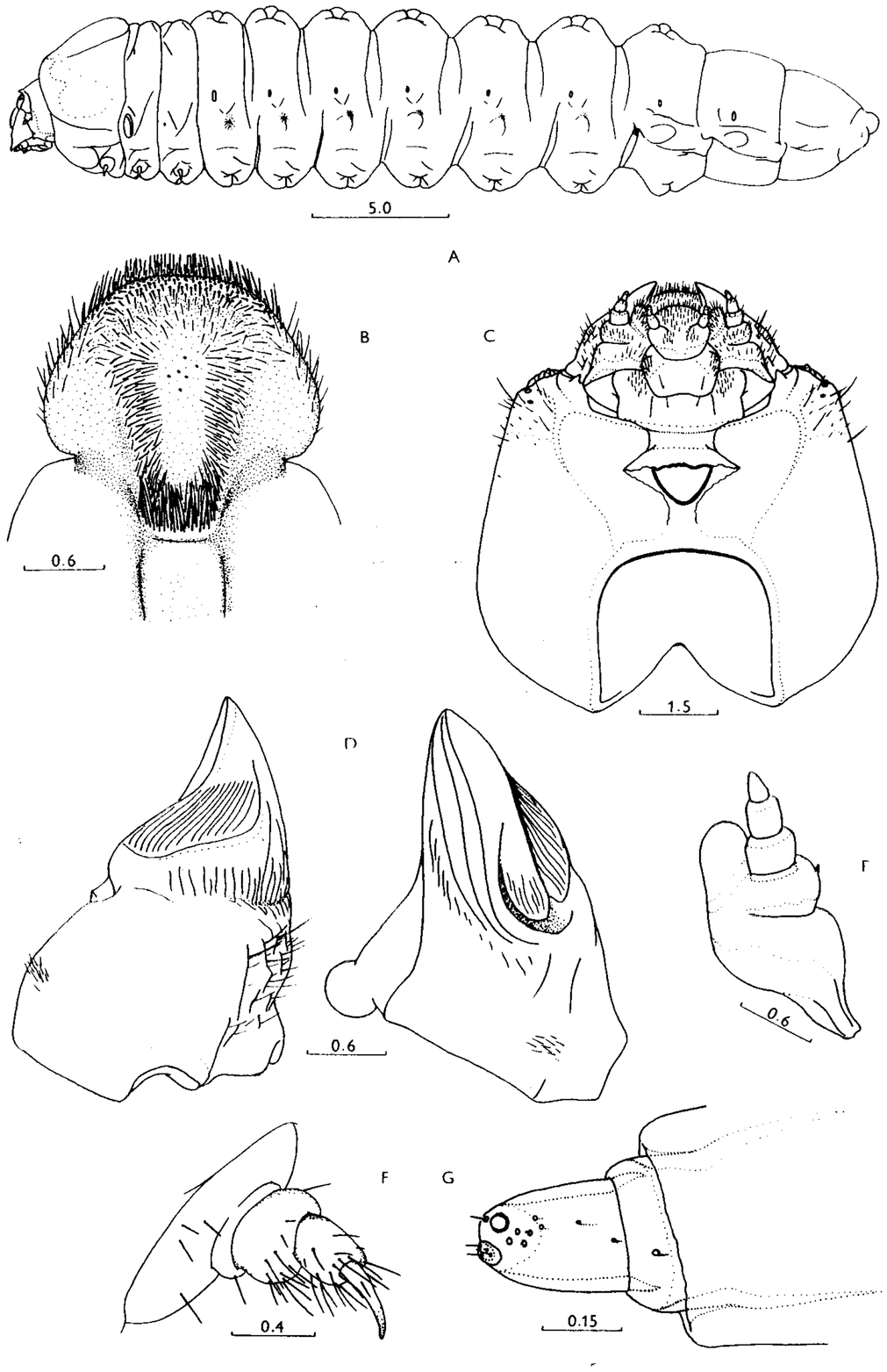
and devoid of setae. Labiomaxillary complex bearing moderately numerous setae, those of ligula and mala slightly stronger than others. Submentum almost not separated from mentum, both largely sclerotized, former with main pair of setae very close to anterior margin. Connecting lobes nearly unsclerotized, with up to about 15–20 setae each. Basal pigmented band of stipes broadly interrupted at lateral extremity. Palpiger somewhat angulate laterally, process absent. Maxillary palps relatively long and slender, segments gradually shortening from 1 to 3, third conical, apical sensory area small. Mala with very broad flattened inner edge (Fig. 161). Mentum without distinguished basal spots or band. Pigmentation of labial palpigers narrow, first palpal segment devoid of setae, second ± cylindrical, slender. Ligula broad, unpigmented, with stout apical and dorsal setae. Hypopharyngeal notch distinct, anterior dorsal portion moderately long, posterior portion with group of setae on each side.

Dorsal prothoracic pigmented band very pale, pronotum irregularly rugose, almost without medial impressed line. Sublateral impressions rather narrow, with distinct accessory transverse impressed lines behind them. Lateral furrows reaching pigmented band. Posterodorsal angle of epipleurum essentially fused with alar lobe. Epipleurum and praesternum with pale anterior pigmented spots. Pleural sulcus strongly S-curved, its lateral extremity deeply but narrowly impressed, without large fovea. Episternum almost unsclerotized, not protuberant. Mediopraesternum well defined (less so at apex). Both halves of coxosternum large, transverse, approaching each other. In younger larvae, discernible microscopic spines can be found on certain regions (sternellar fold, coxosternum, hind angles of mediopraesternum).

Meso- and metathorax generally similar to *Ergates*. Mesothoracic spiracle with marginal chambers present mostly only along upper two-thirds of hind margin.

Legs slightly longer than maxillary palps. Trochanter complete, bearing a few setae. Femur shorter than tibiotarsus, finely pigmented, both segments with numerous medial setae. Praetarsus about as long as tibiotarsus, slender, without setae, its tip pigmented.

Abdomen with typical Prionine ambulatory ampullae, latter almost smooth, in later instars without distinct spines. Spiracles moderately large, narrow, oval, ferrugineous, hind margin with numerous small marginal chambers. First spiracle slightly larger than others, at least twice shorter than mesothoracic spiracle. Radially striate pleural discs present on all six anterior abdominal segments, large on segment 1, smaller, however, distinct on segments 2 to 6. Ninth segment relatively short, hardly longer than eighth. Hind margin of tergum 9 often (particularly in later instar larvae) with two minute flat tubercles (in some specimens they are even finely sclerotized, Fig. 16J) which may prove to be rudimentary urogomphi. (Note: LINSLEY, 1962a, p. 57, writes about *Tragosoma depsarium:* »The larvae suggest those of *Ergates* and differ from *Prionus* in having cerci.« I do not know the source of that statement, but I believe it to be a mistake. According to CRAIGHEAD, 1923, it is the pupa of *Tragosoma* differing by two strong caudal spines from the pupae of North American *Prionus*-



-species, not the larva. CRAIGHEAD never mentioned presence of urogomphi in *Tragosoma* larvae, or in larvae of any North American Prioninae; in fact urogomphi are known in not a single Prionine larva, and if the above described structures of *Tragosoma* larvae were really rudimentary urogomphi, then it is the first record of at least remnants of larval urogomphi in Prioninae. In any case it is quite impossible to say that the *Tragosoma* larva possesses urogomphi - »cerci«.) Anus terminal, anal tube well separate, anal papillae distinct, bearing numerous minute setae, dorsal papilla remarkably protuberant (Fig. 17A), may be slightly sclerotized.

One species recognized in Palaearctics.

Tragosoma depsarium (L., 1767)

Length up to 50 mm.

Host plants: *Pinus* spp. Other conifers sometimes listed (*Picea, Abies*) are not, as far as I know, confirmed by real found of larvae. According to CHEREPANOV (1979), larvae feed in dead, mostly fallen trunks, in decaying sapwood. Development period at least three years. Pupation in the wood, pupae June - early July, adult emergence from the end of June to August.

Distribution: Holarctic. In Palaearctics - coniferous forests of Europe and Siberia.

Material: 11. 7. 1963 Sweden, Dalarna, Näs, one larva from *Pinus,* M. Sláma coll; July 1978 France, Pyrenées occ., Oredon, 5/I, *Pinus,* M. Sláma lgt. et coll; 9. 8. 1973 SU, Baikal region, Khamar-Daban Mts., 5/I, *Pinus,* lgt. D, coll. IS; 5. 8. 1937 Finland, labelled »EH. Ruovesi, Siikakangas«, one larva, U. Saalas lgt., coll. IS; 7. 9. 1950 Sweden, 1/I, *Pinus,* T. Palm lgt. et coll.

Genus *Ergates* SERVILLE, 1832

Type species: *Prionus serrarius* PANZER, 1793 = *Cerambyx faber* L., 1767 (monobasic)

Two species occur in Palaearctics. However, nothing but one exuvia available of *E. gaillardoti.* Since many characters cannot be described from the cast skin, the following generic description is based solely on larvae of the type species, *E. faber.* The differences of *E. gaillardoti* given at the end, however, they are not incorporated in the generic description.

Body short and very robust, setae very short, rusty brown.

Cranium subquadrate (1.1–1.25), moderately depressed (about 2.0), not microgranulate, anterior half yellowish, posterior one unpigmented, mouthframe strongly but rather narrowly sclerotized, dark ferrugineous to almost black. Epicranium with sides slightly to distinctly roundly convex, anterior setae very short and few, cranium widest far behind middle, deeply and rather broadly notched behind (Fig. 17C). Frontal lines (at least in later instar larvae) discernible along whole length,

Plate 17: A — *Tragosoma depsarium,* later instar larva, lateral view. (Setae not figured.) B — — *Ergates faber,* mature, epipharynx. C — *E. faber,* submature, head, ventral view. D — *E. faber,* mature, right mandible, dorsal (left) and medial (right) views. E — *E. faber,* submature, outline of left distal maxilla, lateroventral view. F — *E. faber,* later instar, left middle leg, anterior view. G — *E. faber,* submature, right antenna, ventral view.

S-curved, in young larvae may cross antennal ring, in later instar larvae end blindly just before antennal openings, do not reach anterior cranial margin. Frons moderately long (its medial length about equal to that of dorsal duplicated region), almost flat, at most finely rugose. Regular anterior setae supplemented by at most very few minute accessory ones, except for anterior frontal angles before postcondylar carinae where can be found numerous short setae. Postcondylar carinae very long, sharp, prominent, longitudinally striate, frontal areas before them rather distinctly longitudinally rugose. Frontal carina interrupted in middle, projecting in two pairs of large flat teeth (Fig. 18A). Epistomal carina almost absent in middle, laterally projecting into very large rounded or triangular plates (except for youngest larvae). Mostly six epistomal setae, supplementary setae, if present, mostly smaller. Clypeus narrow, trapezoidal, unpigmented or at most very pale yellowish. Labrum cordate, about as long as broad, feebly convex, largely pigmented except for apical margin which is pale and fringed with short dense setae, more sparse setae present along lateral margins. Two long and usually a few small discal setae. Epipharynx as figured (17B), setae not reaching backwards to sides of hind raised portion, united posteriorly by transverse group of long setae, tormae not very long, oblique, tapering. Pleurostoma dark, feebly raised, without sharp carina, subfossal process mostly very long, conical. Gena finely rugose, intensively pigmented, pigmentation at least as wide (mostly about twice as wide) as pleurostoma. Three (very rarely two) main stemmata on each side, they are distinct, separate, convex, facing forward due to distinctly protuberant gena. Individuals may be found with four main stemmata on one or even both sides (Fig. 18B). One (rarely two) ± distinct dorsal stemmata, ventral stemma from well developed to indiscernible. Hypostomal lines distinct, slightly S-curved, reaching postoccipital line, anterior halves pigmented. Hypostomal sclerites may bear single minute setae. Gula shortly exposed, much narrower than one hypostomal sclerite (Fig. 17C). Metatentorial bridge almost twice as wide as gular bridge.

Antennae moderately long, three-segmented, but third segment much reduced, knob-shaped, in some mature larvae almost incorporated in apical membrane of second segment and hardly distinguishable. Antennal ring projecting into large, often striate shell largely covering connecting membrane (Fig. 18A), latter membrane moderately large. Segment 1 deeply retracted, with at most minute subapical setae, segment 2 (except for very young larvae) much longer than broad, obliquely truncate apically, main sensillum flat, subcircular (Fig. 17G). Mandibles generally similar to *Tragosoma,* but molar portion with dorsal group of short setae (Fig. 17D, usually absent in very young larvae). Submentum markedly sclerotized, mostly with two setae, they are not shifted to border with mentum. Connecting lobes almost unpigmented, in later instar larvae bearing numerous setae. Basal pigmented band of stipes suppressed laterally by large pale protuberant area. Palpiger in most individuals with small laterodorsal microasperate process (Fig. 17E). Maxillary palps comparatively long, segments in later instar larvae ± shortening from 1 to 3, third segment

conical, apical sensory area small, terminal. Mala moderately broad, less sharply carinate than in *Tragosoma.* Mentum separated from submentum, usually with two narrow transverse basal spots, central area sclerotized, anterior angles with up to about 20–30 setae on each side. Labial palpigers extensively pigmented, palps short, first segment with at most 1–2 minute setae. Ligula large, rounded, hypopharyngeal notch very distinct, anterior portion rather short, with dense stout setae, posterior portion with group of setae on each side (Fig. 18C).

Prothorax with pigmented areas of tergum, epipleurum and lateropraesternum at most pale yellowish, their pigmentation homogeneous, not spotted. Most of pronotum finely densely rugose, medial line not impressed. Lateral furrows reaching pigmented band. Sublateral impressions shallow, transverse, supplementary impressed lines behind them present (Fig. 18A). Posterodorsal angle of epipleurum tending to fuse with alar lobe. Mediopraesternal boundary distinct (less so at apex). Episternum almost unpigmented, pleural sulcus gently S-curved. Both halves of coxosternum large, transverse, almost meeting (not visible in contracted larvae).

Meso- and metanotum in young larvae with very fine microscopic spines, disappearing in mature larvae. Postnotal fold well developed (Fig. 18A). Metanotum with both transverse lines distinct, separate, not X-shaped. Scutum I very distinct on metathorax. Mesothoracic spiracle moderately large (cf. *Megopis*), elongate oval, slightly protruding into prothorax, with small marginal chambers, their number and distribution extremely variable. Rudimentary metathoracic spiracle discernible. Transsternal lines distinct.

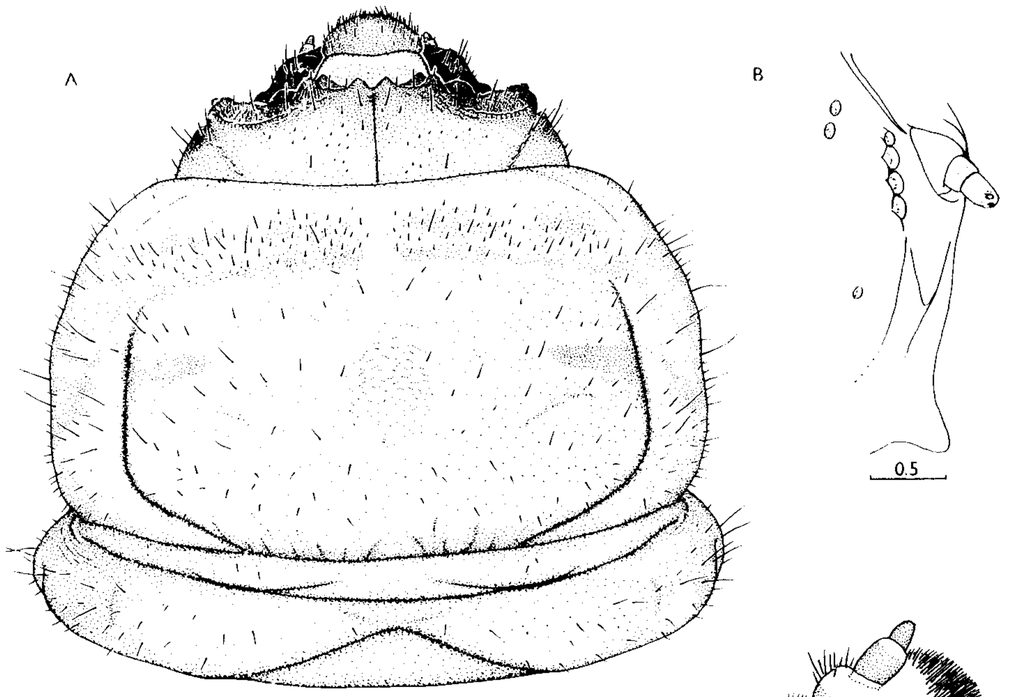
Legs slightly longer than maxillary palps. Trochanter distinct, complete, with a few setae, remaining three segments subequal in length, or femur somewhat shorter; femur and tibiotarsus almost unpigmented, with numerous setae, most of them from inner side. Praetarsus slender, conical, apex sclerotized; sometimes with one or even several minute setae (Fig. 17F).

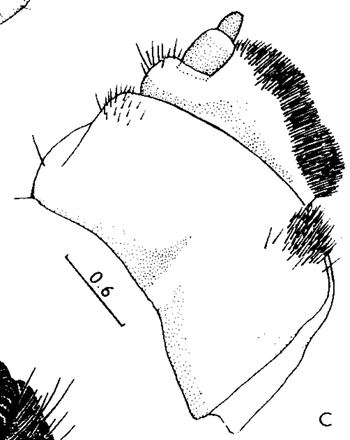
Typical Prionine ambulatory ampullae, finely rugose, without microscopic spines. First abdominal spiracle only slightly larger than others, rarely less than twice shorter than mesothoracic spiracle. Abdominal spiracles with up to about 25 marginal chambers along hind margin. Pleural discs present on all six anterior segments, gradually decreasing in size from 1 to 6. Ninth segment relatively short, just slightly longer than segment 8. Anus terminal, anal segment sharply separated from segment 9, dorsal anal papilla not remarkably protuberant.

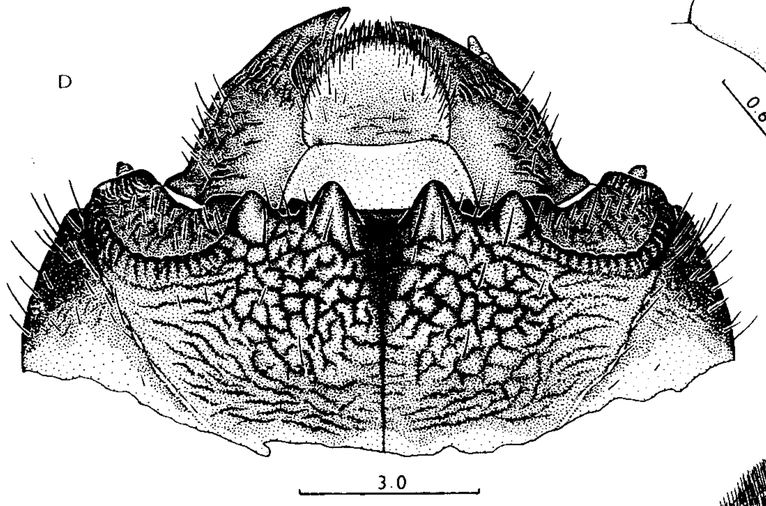
Ergates (s. str.) *faber* (L., 1767)

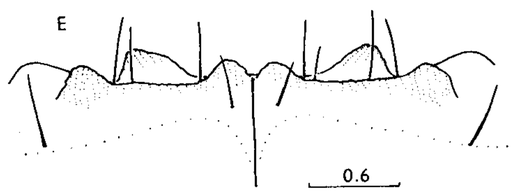
Length up to 70–80 mm.

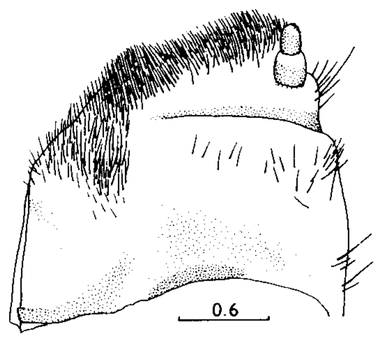
Host plants: *Pinus, Picea, Abies.* Data about development in deciduous trees (PLAVILSHCHIKOV, 1932, and cited also in other papers) are doubtful and should be confirmed. *Pinus* seems to be preferred. Larvae live in dead wood, mostly of greater diameter - standing or fallen trunks, stumps, often in underground parts of the tree. Development period apparently at least











three years, may be much prolonged by dessication of the wood. Pupation in later spring and summer in the wood, flight in summer.

Distribution: Central and South Europe incl. Caucasus; North Africa, Asia Minor.

Material: 46 larvae from Spain, France, Greece, Turkey, CS, SU (Krasnodar region), from *Pinus* and *Abies*, coll. IS, S, M. Sláma, E. Vives, National Museum Prague.

Ergates (subg. *Callergates* LAMEERE, 1906) *gaillardoti* CHEVROLAT, 1854

Mature larva distinctly differs from that of *E. faber*. Cranium extremely broadly and heavily sclerotized anteriorly (Fig. 18D). Frons strongly sclerotized except for posterior angle, very roughly irregularly rugose, gena very dark, almost three times as wide as pleurostoma. All four teeth of frontal carina extremely large, particularly their medial pair conical, non-flattened, lateral parts of epistomal carina, however, much smaller than those of *E. faber*. Epipharynx almost without medial transverse group of long setae. Pleurostoma with relatively distinct carina. Dorsal stemma small, ventral stemma invisible. Palpiger process absent. Mala broader, sharply carinate. Hypopharyngeal notch situated more posteriorly. Spiracles very strongly sclerotized. Pleural discs very distinct. Ninth abdominal segment around anal tube distinctly rugose and finely sclerotized. Mature larva very large, about 100 mm.

Host plant: *Pinus*.

Distribution: Syria, Turkey.

Material: 6. 6. 1984 Turkey, Icel, Namrun (1200 m.), one exuvia of mature larva from *Pinus*, G. Sama lgt., coll. S.

Genus *Megopis* SERVILLE, 1832
Subgenus *Aegosoma* SERVILLE, 1832

Type species: *Prionus scabricornis* SCOPOLI, 1763 (THOMSON design., 1864)

Body moderately elongate, with very short ferrugineous setae.

Cranium subquadrate (1.1—1.2), moderately depressed (1.8—2.0). Mouthframe heavily sclerotized, remaining surface smooth, yellowish to unpigmented. Cranium widest behind middle, sides moderately convex (Fig. 19A). Cranium only very shallowly emarginate posteriorly. Frontal lines in later instar larvae visible along whole length, neither angulate nor S-curved, frons almost triangular. Frontal lines anteriorly not intersecting antennal ring, passing below it and reaching anterior

Plate 18: A — *Ergates faber*, later instar, head, pro- and mesothorax, dorsal view. B — *E. faber*, diagrammatic illustration of pleurostoma, gena and antenna of a specimen with 7 stemmata on right side, lateral view. C — *E. faber*, later instar, distal labium, lateral view (from left side). D — *E. gaillardoti*, anterior part of head of an exuvia of mature larva, dorsal view. (Note that anterior sections of frontal lines are non-functional.) E — *Megopis sinica*, later instar, anterior frontal margin, dorsal view. F — *M. scabricornis*, later instar, distal labium, lateral view (from right side).

cranial margin. Frons short, shorter medially than dorsal duplicated cranial region, almost smooth, broadly impressed at base, convex in anterior half. Postcondylar carinae well developed. Frontal carina prominent, narrowly interrupted in middle, with well developed medial and ± distinct lateral pairs of flat rounded or triangular teeth (Figs 18E, 19A), dorsal face finely longitudinally striate. (In very young larvae frontal carina almost smooth and not toothed.) Epistomal carina projecting laterally over clypeus as rounded or triangular plates (in young larvae also reduced). Mostly six epistomal setae. Clypeus narrow, trapezoidal, emarginate anteriorly, basal half and lateral margins yellow. Labrum (Figs 19D, E) subcircular or indistinctly cordate, feebly convex, pigmented except for apical margin (but only basal one-third dark, other pigmentation rather pale). More or less numerous, occasionally rather long marginal setae present, two stronger and several smaller discal setae. Epipharyngeal setae reaching far behind (Fig. 19C), tormae long, running along sides of hind raised portion. Pleurostoma very dark, with distinct vertical ridge, subfossal process usually robust, prominent, conical, more rarely shortened and blunt. Genal pigmentation at most as broad as pleurostoma. Three distinct convex subcontiguous main stemmata with distinct pigment spots, in later instars facing anteriorly due to genal protuberance. Several specimens have been found with four main stemmata on one or both sides. Dorsal and ventral stemmata inconspicuous, in mature larvae often invisible. Hypostomal lines distinct, ± reaching postoccipital line, almost not curved posteriorly, anterior one-third to one-half pigmented. Gula completely covered by postgular lobe, much narrower than each hypostomal sclerite. Metatentorial bridge about twice as wide as gular bridge.

Antennae moderately long, three-segmented. Antennal ring projecting over connecting membrane. Segment 1 without setae, segments 2 and 3 ± cylindrical, brightly pigmented, in young larvae about as long as broad, in later instars slightly longer than broad. Main antennal sensillum flat, broadly oval. Mandible with border zone striate. Apical part with three distinct inner keels, inner plate small, reduced, with only two to three indistinct ridges; cutting edge not continuous, its long anterior section posteriorly curved and running on dorsal surface (this, as well as other mandibular details, may be indistinct or lost in abraded mandibles). Dorsal plate modified, with two or three coarse ridges, sometimes narrowly indistinctly striate along cutting edge. Lateral face of basal portion coarsely rugose, with numerous setae, remaining surface smooth, glabrous. Submentum intensively pigmented, its setae shifted forward, lying ± right on border with mentum. Connecting lobe almost unpigmented, up to several tens of setae in large mature larvae. Basal pigmentation of stipes absent in lateral one-third. Palpiger process absent. Mala with broad carinate inner edge. Maxillary palp relatively short and stout, segments slightly decreasing in length from 1 to 3, third segment robust, with unusually distinct broad shallow lateral impression, apical sensory area rather large. Mentum with large central yellowish area, no basal spots visible in ventral view, anterior angles densely setose. Pigmentation of both labial palpigers ± connected, palps short, segments'

lengths subequal, first segment may have 1–2 dorsal subapical setae. Ligula broad, without distinct pigmentation, hypopharyngeal notch ± absent, anterior dorsal portion long, both anterior and posterior portions densely setose (Figs 18F, 19B).

Pigmented areas of prothoracic tergum, epipleurum and lateropraesternum pale, in later instar and particularly mature larvae non-homogeneous, spotted (mainly muscle attachment areas pigmented). Pronotum behind pigmented band finely rugose, rather distinct medial impressed line reaching posterior margin. Sublateral impressions very shallow, moderately oblique. Lateral furrows deep, reaching pigmented band. Posterodorsal epipleural angle connected with epipleurum, sharply and completely separate from alar lobe. Episternum sclerotized, yellow-orange, without distinct protuberance, pleural sulcus strongly S-curved. Mediopraesternum poorly defined, anteriorly fused with lateropraesternum. Both halves of coxosternum large, transverse, approaching (however, not meeting) each other. Sternellar fold comparatively narrow, reduced.

Meso- and metanotum with at most very fine indistinct microscopic spines. Postnotum well developed. Both transverse lines of metanotum almost fused and X-shaped. Scutum I defined on metathorax. Mesothoracic spiracle large, remarkably (in mature larvae about 2–3 times) longer than maxillary palp, slightly protruding into prothorax, very narrow, deeply pigmented, most of hind margin (and often upper portion of anterior margin as well) with great number of very small marginal chambers. Rudimentary metathoracic spiracle very distinct. Transsternal lines present, lines dividing basisternum obscure, those of metasternum almost lacking.

Legs short, hardly longer than maxillary palps. Trochanter extremely reduced, distinct only from inner side, with at most 1–2 setae. Three distal segments subequal in length, femur and tibiotarsus laterally pigmented, in later instars with numerous setae from inner side. Praetarsus stout, pointed, rarely with one short seta; at most its tip pigmented.

Typical Prionine ambulatory ampullae, sparsely finely rugose. Spiracles similar to mesothoracic one, marginal chambers relatively slightly larger, restricted to hind margin. First spiracle much larger than remaining ones, much less than twice (about 1.5 times) shorter than mesothoracic spiracle. Large pleural discs on first segment, those of segment 2 and esp. 3 small, much smaller than spiracles of their segments, discs 4 to 6 absent. Segment 9 much longer than 8, anal segment poorly separate from segment 9. Anus terminal, shifted very slightly dorsad, anal papillae distinct, their inner lips with remarkably numerous minute setae, dorsal papilla not more protuberant than remaining two.

Larvae of two species at my disposal:

1(2)! First segment of labial palps without setae. Dorsal face of antennal shell at most feebly incontinuously microreticulate, often distinctly striate. West Palaearctics . . . *scabricornis*

2(1)! First segment of labial palps with 1–2 dorsal marginal setae. Dorsal face of antennal shell distinctly regularly microreticulate. Far East . . . . . *sinica*

Megopis (Aegosoma) scabricornis (SCOPOLI, 1763)

Extremely similar to the following species. In addition to the key differences (much more specimens of *M. sinica* needed to confirm their validity), labrum with setae relatively shorter in corresponding instars, mostly more numerous (Fig. 19E). Frontal and epistomal carinae mostly with less prominent teeth (Fig. 19A). Microscopic spines on pterothoracic nota extremely indistinct, particularly in later instar larvae. Length up to about 70 mm.

Host plants: Polyphagous on deciduous trees, no records from conifers known to me. The larva feeds in moist decaying wood of greater diameter, standing or fallen, frequently in dead parts of living trees. Pupation in the wood in spring/summer of the year of emergence. Several-year life-cycle.

Distribution: Europe except the North, Asia Minor, Syria, Iran, Caucasus, Transcaucasia.

Material: 1977–78 CS, Slovakia, Štúrovo env., +/I, *Salix, Populus, Juglans, Prunus,* lgt. et coll. S; 19. 8. 1976 Bulgaria, Ropotamo, Arkutino, 9/–, *Celtis australis,* lgt. et coll. S; 27. 6. 1983 SU, Caucasus, Zakataly, 1/–, *Fraxinus*, lgt. et coll. S; March–April 1980 SU, Krasnodar, 10/I, *Salix,* lgt. A. Miroshnikov, coll. IS.

Megopis (Aegosoma) sinica (WHITE, 1853)

Very similar to *M. scabricornis*. In addition to the key characters, labrum with setae longer and less numerous (Fig. 19D), frontal and epistomal carinae with slightly larger teeth (Fig. 18E), microscopic spines on pterothoracic nota slightly more distinct, mouthframe very strongly sclerotized, pitchy. Only later instar larvae available (one complete larva, one incomplete head), and all the above differences are doubtful, in fact the author believes they would turn invalid if better material was available. The distribution is the best character to employ.

Host plants: T. KOJIMA (1931) listed *Populus* spp., *Fraxinus mandshurica* var. *japonica, Abies firma, A. sachalinensis, Pinus densiflora, Mallotus japonicus, Salix babylonica* (there are surely others known today). Apparently even more polyphagous than the preceding species. Judging from the paper of T. KOJIMA (l.c.), habits are essentially similar to *M. scabricornis,* somewhat varying according to the species and condition of the tree attacked.

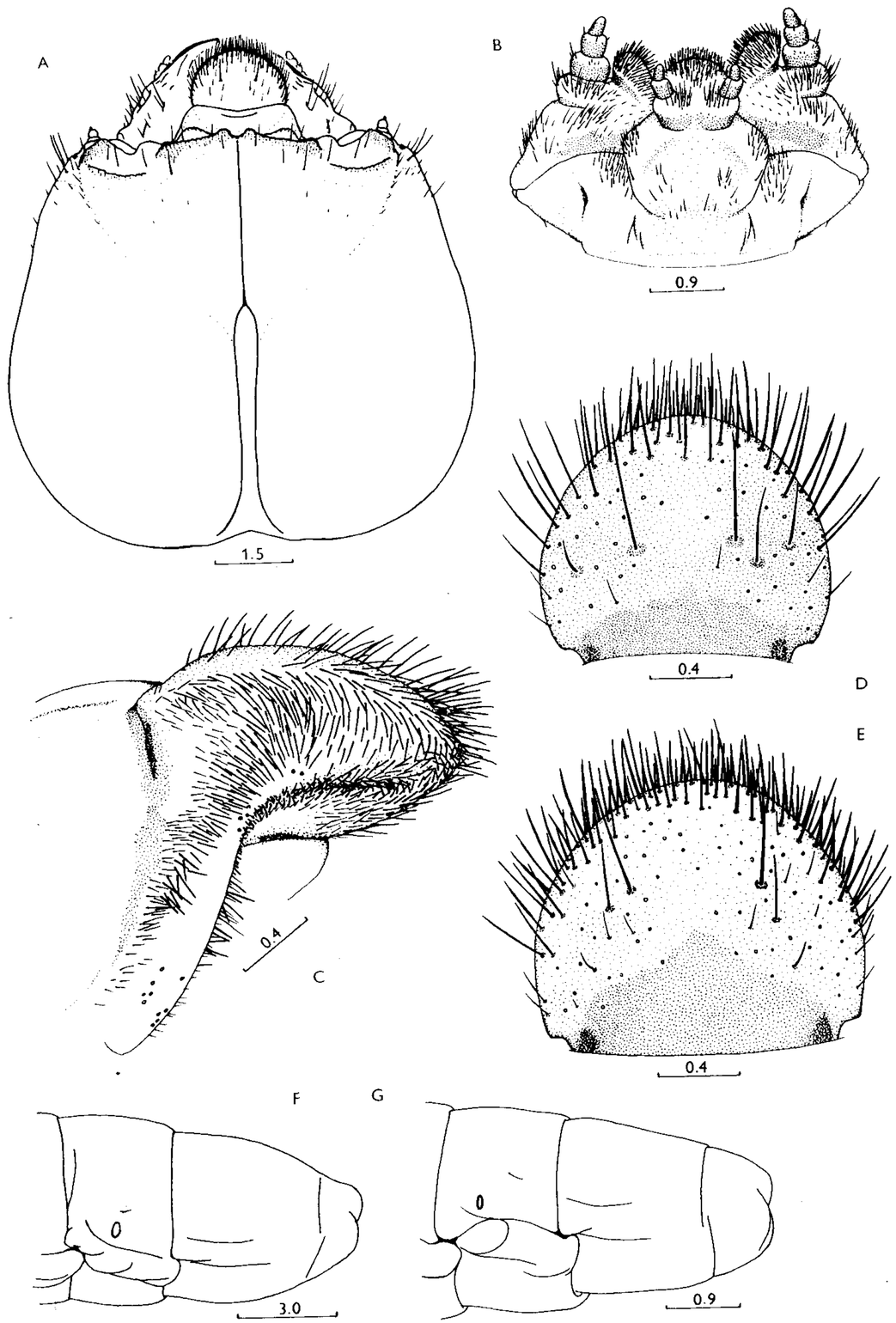
Distribution: Far East (incl. USSR, China, Korea, Japan).

Material: 31. 8. 1951 Japan, Honmoku, Yokohama, one larva and one damaged head, coll. S. Nakamura.

Genus *Prionus* MÜLLER, 1764 (sensu lato, and including *Dorysthenes* VIGORS, 1826)

The genus *Prionus* includes a great number of rather diverse species. Larvae of only a few species available, and thus the larval subgeneric classification and characters should be considered

Plate 19: A – *Megopis scabricornis,* later instar, head, dorsal view. B – *M. scabricornis,* later instar, labiomaxillary complex, ventral view. C – *M. scabricornis,* later instar, epipharynx, lateroventral view. D – *M. sinica,* later instar, labrum. E – *M. scabricornis,* later instar, dtto. F – *Prionus coriarius,* later instar, outline of abdominal segments 8 to 10, lateral view. G – *P. komarovi,* later instar, dtto.



provisional. As long as this broad concept of the genus *Prionus* is accepted, the genus *Dorysthenes* must be included in *Prionus*, as larvae of the former are apparently more similar to those of *Prionus* s. str. than are e.g. the larvae of *Prionus komarovi* or *P. brachypterus*.

Type species: *Cerambyx coriarius* L., 1758 (LATREILLE design., 1810)

Body moderately elongate, with short ferrugineous to unpigmented setae.

Cranium relatively narrow, subquadrate (1.0–1.1), moderately depressed (1.7 to 1.95), widest behind middle or parallel-sided, not microgranulate, mouthframe strongly (in some species extremely broadly and heavily) sclerotized. Epicranial halves at most feebly convex, with very few anterior setae. Cranium rather deeply notched behind. Frontal lines ± distinct, S-curved, not reaching anterior cranial margin, entering antennal openings (from sides or from below), or in later instar larvae often ending blindly near those openings. Frons short (at most as long medially as dorsal duplicated region, mostly distinctly shorter), moderately impressed behind or almost flat, in later instars of some species ± coarsely rugose. Four or five pairs of main anterior frontal setae, other setae very small or absent. Postcondylar carina not very long (mostly not reaching antennal shell), low. Frontal carina of varying shape according to species. Epistomal carina projecting far over clypeus except for *Psilotarsus* where reduced. In young larvae mostly six epistomal setae; later instar larvae of some species often lacking medial pair. Clypeus broad, very short, rapidly tapering, unpigmented. Labrum broad, at least slightly transverse, half-circular, cordate or oval, rather flat. Basal pigmentation of varying extent, but anterior half always unpigmented and setose, main pair of discal setae sometimes differing by greater size. Anterior epipharyngeal region may be slightly sclerotized, posterior raised portion sometimes with small medial sclerotized area. Setae reaching backward along anterior half of hind portion. Tormae long, ± interrupted. Pleurostoma raised, heavily sclerotized, with vertical carina, subfossal process prominent, stout. Genal pigmentation at least as broad as pleurostoma. Stemmata absent, but genal protuberance (once directing main stemmata forward) ± preserved, making gena shouldered or even somewhat carinate behind pleurostoma. Hypostomal lines ± distinct, hardly reaching postoccipital line, straight to gently incurved posteriorly, at most their anterior halves pigmented. Gula entirely covered, broad, about as wide as one hypostomal sclerite. Metatentorial bridge about 1.5 to 2 times wider than gular bridge.

Antennae relatively short, three-segmented. Antennal ring projecting over connecting membrane, latter relatively large, antennae deeply retractile. Segment 1 devoid of setae, segment 2 in later instar larvae about as long as broad or slightly longer, cylindrical or somewhat tapering. Segment 3 short, rarely longer than broad, often transverse to knob-shaped (Fig. 20C). Main sensillum large, usually elliptical in apical view, in *P. komarovi* very large and distinctly roundly protuberant (Fig. 20D). Mandibles remarkably individually variable. Border zone sometimes striate. Apex and dorsal angle rather blunt, connected by simple continuous cutting edge.

Three inner keels present, ventral one sometimes shortened, reduced or almost absent. Inner striated plate absent, only its reduced curved marginal ridge present. Dorsal striated area equally absent, dorsal face with one or two ± prominent oblique ridges. Lateral face of basal portion ± coarsely rugose, bearing relatively few setae, remaining surface either smooth, or transversely loosely striate, molar part without setae. Labiomaxillary complex relatively large (Fig. 20A), with numerous very short setae. Mentum and submentum medially fused, in some species with common yellowish area, submentum with setae not moved to anterior border. Connecting lobes large, unpigmented, up to several tens of setae each (depending on species). Cardo often with minute sublateral seta. Stipes with basal band complete, suppressed laterally by large pale spot, but not interrupted. Outer face of palpiger from rounded to rather prominent and flattened (Fig. 21D), process absent, or rarely minute tubercle present (Fig. 21E). Maxillary palps short, robust, segments subequal in length or segment 2 (!) shorter, segments 1 and 2 often transverse. Segment 3 at most moderately tapering, apical sensory area extremely large. Mala relatively narrow, inner side feebly carinate. Mentum with narrow transverse paired basal spots, anterior angles densely setose. Pigmentation of both labial palpigers often connected. Ligula covered with dense, very short and stout setae, may bear lateral sclerotized spots. Hypopharyngeal notch distinct, anterior dorsal labial portion very short, both anterior and posterior portion densely setose. Labial palps very short, robust, first segment sometimes with several setae, second segment with apical sensory area unusually large.

Prothorax relatively small, narrow and abruptly tapering anteriorly in comparison with other Prioninae. Prothoracic pigmentation from bright orange to absent. Pronotum irregularly rugose (seldom almost smooth), medial line almost not impressed, lateral furrows distinct, reaching pigmented band (if present), sublateral impressions indistinct to absent. Posterodorsal epipleural angle not fused with alar lobe. Mediopraesternum well defined, border line somewhat obscured at apex. Episternum moderately sclerotized, with longitudinal protuberance, pleural sulcus almost straight, without lateral fovea. Coxosternal halves large, transverse, almost meeting each other.

Meso- and metanotum in later instar larvae with microscopic spines indistinct or absent. Postnotal fold well developed. Praescuto-scutal and scuto-scutellar lines of metanotum distinct, narrowly separated or almost X-shaped. Scutum I feebly defined on both segments. Mesothoracic spiracle slightly protruding into prothorax, very small, at most about 1.5 times longer than maxillary palp, rather broadly elliptical, marginal chambers from distinct to absent. Metathoracic spiracle discernible. Transsternal lines distinct, may be slightly reduced about middle, basisternum with oblique lines present or obscure.

Legs moderately long, slightly longer than maxillary palps. Trochanter unequal, medial portion large, with basal sclerotized crescent and with row of several setae, lateral portion extremely reduced. Femur about as long as tibiotarsus, both laterally

± pigmented, bearing dense stout setae. Praetarsus slender, apical one-third sclerotized, setae absent.

Typical Prionine ambulatory ampullae, at most finely rugose. Spiracles small, broadly oval, with or without marginal chambers. Spiracles 1, 7 and 8 very slightly larger than others, first spiracle as long as, or somewhat longer than one-half of mesothoracic spiracle. Extremely large and distinct pleural discs on all six anterior segments, rather sharply delimited, densely radially striate, often with fine marginal sclerotization, first disc usually largest, even disc 6 as large as, or usually larger than its spiracle. Segment 9 slightly longer than 8. Anal segment finely separate from segment 9, anus terminal, anal papillae prominent.

Larvae of seven species available (see also Supplement to *Prionus*). In addition to this, larvae of two species of *Dorysthenes* at my disposal from China and Morocco, larva of the former should be essentially similar to *D. paradoxus* which probably occurs in the USSR (LOBANOV, DANILEVSKY et MURZIN, 1981).

1(2) Main antennal sensillum very large, remarkably protuberant (Fig. 20D). Anal tube extremely large (Fig. 19G). (Sg. *Polyarthron* SERVILLE, 1832, or this species classified in a separate sg. *Microarthron* PIC, 1900.) . . . . . *komarovi*

2(1) Main antennal sensillum smaller, flat (Fig. 20C). Anal segment not enlarged (Fig. 19F).

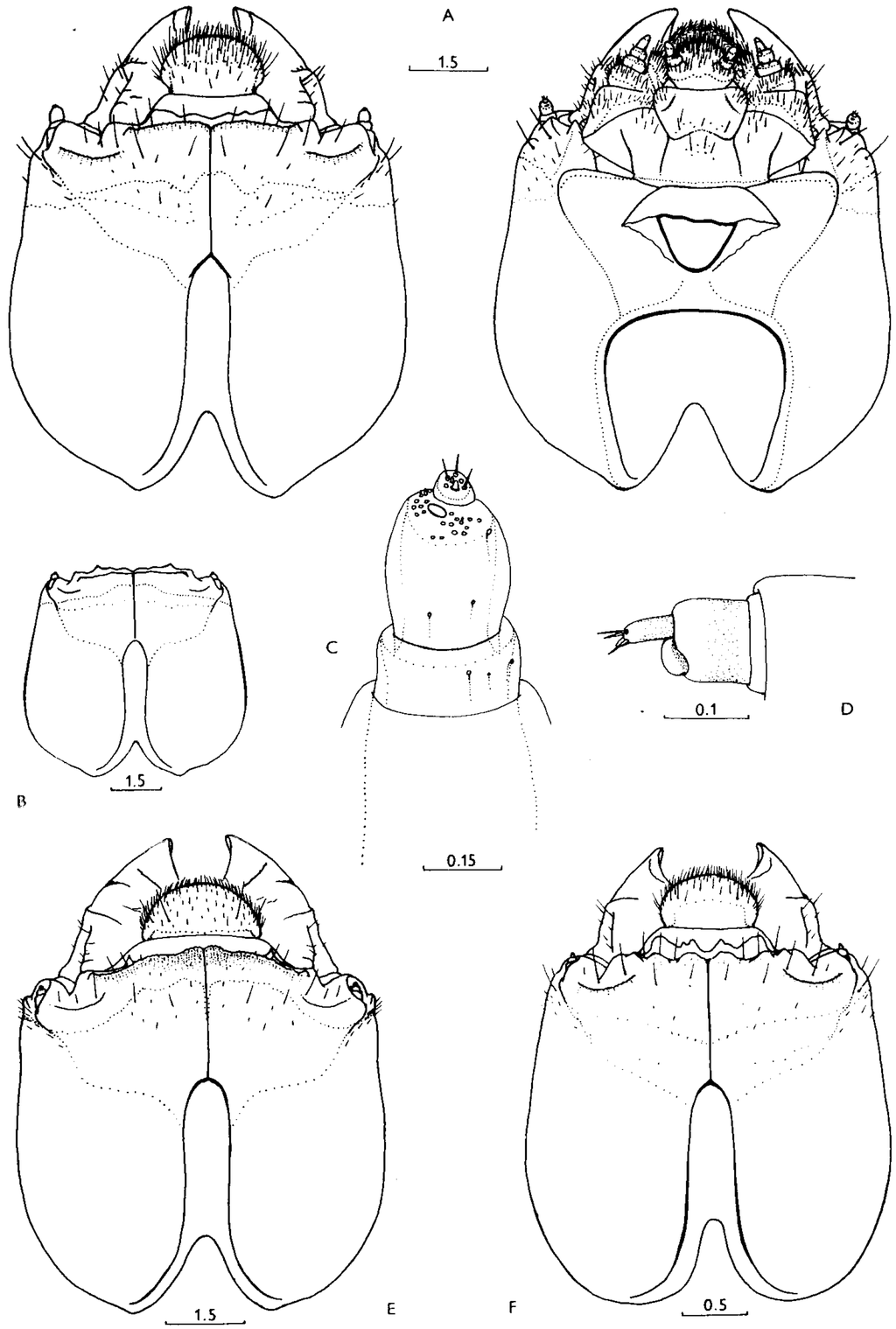
3(4) Labrum half-circular, almost not constricted at base, with very short setae and very narrow basal pigmented band. Mouthframe (particularly anterior frontal margin) narrowly pigmented. Frontal carina extremely sharp, prominent, projecting obliquely upwards, extended beyond anterior frontal border (it must be expected less prominent in younger larvae which are not available). Epistomal carina reduced, with small slender lateral teeth (Fig. 20E). Larvae feeding on roots of herbaceous plants. (Sg. *Psilotarsus* MOTSCHULSKY, 1860.) . . . . . *turkestanicus, ?brachypterus*

4(3) Labrum transversely oval to slightly cordate, distinctly constricted at base, setae longer, basal pigmented area broad (Figs 21B, C). Frontal carina much less prominent, epistomal carina projecting (at least in later instar larvae) far over clypeus, lateral angles broad (Figs 20A, 21A). Mouthframe more extensively pigmented at least in frontal region. Larvae in roots of trees or shrubs, but occasionally may be found in soil.

5(6) Third antennal segment (in two available almost mature larvae) slender, cylindrical, about as long as broad. Palpiger with distinctly prominent, somewhat flattened lateral face bearing ± distinct tubercle (Fig. 21E). (*Dorysthenes* VIGORS, 1826). All pigmentation very pale and restricted, mentum and submentum unpigmented, prothoracic band essentially absent (sg. *Cyrtognathus* FALDERMANN, 1835) . . . . . *hydropicus (?paradoxus)*

6(5) Third antennal segment in later instar larvae very short, much shorter than broad, knob-shaped (Fig. 20C, in very young larvae may be cylindrical and as long as broad, then very robust). Palpiger with lateral face rounded, sometimes slightly angulate, but almost never as prominent as in *Dorysthenes*, or with tubercle (Fig. 21D). Pigmentation more extensive, mentum and submentum yellowish, prothoracic band yellow to orange.

Plate 20: A — *Prionus coriarius*, submature, head, dorsal (left) and ventral (right) views. B — *P. insularis*, later instar, outline of cranium, dorsal view. C — *P. coriarius*, later instar, left antenna, ventral view. D — *P. komarovi*, later instar, left antenna, laterodorsal view, diagrammatic (showing large transverse protuberant main antennal sensillum). E — *P. ?turkestanicus*, later instar, head, dorsal view. F — *P. komarovi*, later instar, dtto.



7(10) Labrum longer, somewhat cordate, with relatively shorter and denser setae (Figs 21A, C; in preserved larvae labrum often partly retracted!). Frons in later instar larvae rather densely often roughly irregularly rugose (Fig. 21A). In dry areas. (Sg. *Mesoprionus* JAKOVLEV, 1887.)

8(9) Prothoracic band bright orange . . . . . *?besicanus*

9(8) Prothoracic band ± pale, yellow . . . . . *asiaticus, angustatus*

10(7) Labrum shorter, ± elliptical, setae in corresponding instars longer and less numerous (Figs 20A, 21B). Frons rarely more distinctly rugose, then rather sparsely so. In more humid forest areas. (*Prionus* s. str.) . . . . . *coriarius, insularis*

The subgeneric classification is rather unclear, the genus should be revised on the world basis.

Prionus (s. str.) *coriarius* (L., 1758)

Cranium slightly diverging posteriorly, deeply notched behind (Fig. 20A). Frontal lines enter antennal openings from sides, in later instars end blindly. Frons distinctly impressed at base and convex anteriorly, never as roughly and densely rugose as usual in *Mesoprionus*. Anterior frontal half dark. Frontal carina low, sometimes with indistinct lateral tooth. Epistomal carina in later instar larvae large, from smoothly emarginate to divided in two pairs of broad, rounded lobes. Mostly six epistomal setae. Labrum short, distinctly transverse, ± oval bearing less numerous longer stout setae. Gena rarely carinate, mostly roundly shouldered. Hypostomal lines usually gently curved behind. Third antennal segment in later instar larvae very short, knob-shaped. Main antennal sensillum small, flat. Labiomaxillary complex with relatively long setae (Fig. 21D), maxillary palpiger mostly rounded, almost never with anterolateral tubercle, mentum and submentum pale yellowish. Pigmented areas of prothorax at least in later instar larvae bright yellow-orange. All spiracles with distinct marginal chambers (very small in mature larvae). Legs largely brightly pigmented. Anal segment not enlarged, anal papillae with very few setae. All body setae rather stout, ferrugineous. Length up to 70 mm.

Host plants: Polyphagous on both coniferous and deciduous trees. Larvae feed almost exclusively underground, rarely occur above ground level; in roots or stem base, in dead, often decaying wood. Mature larvae generally leave the wood and pupate in soil in a cocoon constructed from soil and wood particles. Pupation in early summer, emergence in July to August. Several-year life-cycle. Not in dry semidesert areas - a forest species.

Distribution: Europe, West Siberia, Caucasus, Transcaucasia, North Iran, Asia Minor, North Africa.

Material: About 35 larvae from Spain, CS and SU (Tula near Moscow, Krasnodar region. East Caucasus - Caspian coast), coll. E. Vives, M. Sláma, S. and IS.

Prionus (s. str.) *insularis* MOTSCHULSKY, 1857

Extremely similar to *P. coriarius,* differing by its distribution. No reliable morphological differences have been found, those mentioned by CHEREPANOV (1979) turned out invalid in our material. In the two available larvae, and in available illustrations, the posterior cranial notch is slightly more shallow than in almost all larvae of P. coriarius examined for that character (Fig. 20B). Length up to 70 mm, T. KOJIMA (1931) gives 82.5 mm.

Host plants: Apparently as polyphagous as the preceding species. Judging from papers by T. KOJIMA and CHEREPANOV (l.c.), bionomics are very similar, too. KOJIMA mentioned pupation in the wood, which might have been caused by lack of searching for pupae in soil (some individuals of *P. coriarius* may also pupate in wood).

Distribution: Far East.

Material: 14. 4. 1950 Japan, Tokyo, Meguro, 2 larvae, lgt. et coll. S. Nakamura.

Prionus (Mesoprionus) angustatus JAKOVLEV, 1887

Similar to *P. coriarius,* larvae rather morphologically variable, nevertheless, ± distinctly differing by certain characters. Central frontal area almost flat. Gena and anterior frontal region broadly pigmented, rather dark. Frons in later instar larvae densely, often rather coarsely rugose. Medial pair of epistomal setae very often lacking. Labrum longer, with relatively shorter and much more numerous setae. Gena in later instars often sharply carinate. Posterior halves of hypostomal lines ± straight. Labiomaxillary complex with relatively shorter and denser setae. Prothorax with pigmented areas pale, yellow. Marginal chambers very few, extremely small, esp. in mesothoracic spiracle may be indiscernible, abdominal spiracles mostly with less than 10 chambers along very short middle section of hind margin. Body setae thinner, shorter, rather pale. Available larvae up to 50 mm, much larger specimens may undoubtedly occur.

Host plants: *Haloxylon* and *Calligonum* known. Larvae in roots. According to M. L. Danilevsky, mature larva tunnels freely through the soil, also pupating there.

Distribution: Transcaspia. According to M. L. Danilevsky, this species has not been found north of the mouth of Syr-Darya river.

Material: May 1973 SU, Turcmenia, Dzhilikum, 3/−, *Haloxylon,* B. M. Mamaev lgt., coll. IS; 22. 3. 1978 SU, Tadzhikistan, Tigrovaya Balka, 1/−, *Calligonum,* lgt. D, coll. IS (larvae have not been reared, their determination is based on the collecting sites - there should be no other large Prioninae; it seems possible that there are more than one species covered by the species name *angustatus*).

Prionus (Mesoprionus) asiaticus FALDERMANN, 1837

Extremely similar to the preceding species, no reliable morphological differences have been found. As far as known, the two species differ by their distribution. Spir-

acles with more distinct and more numerous marginal chambers, in abdominal spiracles almost along whole hind margin, much more than 10 distinct chambers in later instar larvae. Length up to 75 mm.

The larvae were found in dead underground parts of *Ficus carica,* in dry, almost semidesert situation. At least three-year life-cycle. Pupation unobserved, probably in soil.

Distribution: NW from the Caspian Sea: SE of the European part of the USSR, East Caucasus, East Transcaucasia. According to M. L. Danilevsky, this species has not been found east of the Ural river, so that it is apparently geographically isolated from *P. angustatus.*

Material: 19.—20. 6. 1983 SU, Azerbaidzhan, Gobustan, 5/—, *Ficus,* lgt. et coll. S. The larvae also not reared; there should be two *Prionus*-species in the area, *P. coriarius* and *P. asiaticus.* The larvae differ markedly from larvae of the former and are very similar to the supposed larvae of *P. angustatus* and *P. besicanus.*

Prionus (Mesoprionus) ?besicanus FAIRMAIRE, 1855

Very similar to *angustatus* and *asiaticus.* Differs conspicuously by very broad bright orange prothoracic pigmented band. Length of the only one available fixed larva 45 mm.

Food plant: Probably *Platanus.* Two larvae (one still living) found in soil around roots of this tree.

Distribution: East of Mediterranean area (SE Bulgaria, Greece, Turkey, Syria, Cyprus).

Material: June 1984 Greece, Creta, Kare, one larva in soil under *Platanus,* M. Sláma lgt. et coll. Adults not reared. The larva clearly belongs to the group *asiaticus-angustatus.* No *Prionus* apparently known from Creta so far, but *P. besicanus* occurs in all nearest areas (Greece, Turkey, Cyprus) as a single representative of the subgenus *Mesoprionus.* However, as the fauna of Creta is somewhat endemic, it could be well some other (then probably undescribed) species.

Prionus (Psilotarsus) turkestanicus SEMENOV, 1888

Rather dissimilar to *Prionus* s. str. Cranium (Fig. 20E) very narrow, almost parallel-sided, deeply notched behind. Frontal lines running close along margin s of antennal openings, entering them ± from below. Mouthframe relatively narrowly pigmented, particularly frons with only narrow dark anterior margin, genal pigmentation about as broad as pleurostoma. Frons slightly convex, very finely rugose, frontal carina extremely prominent, very sharp, curved, projecting obliquely upwards, overreaching anterior frontal margin (it is to suppose that in young larvae it would be less prominent). Epistomal carina short, with very sharp and slender lateral processes (again in young larvae probably less distinct). Labrum as described in species key, setae remarkably short, except for a few longer ones (generally, most of both body and head setae very short, and almost unpigmented). Gena abruptly protuberant, slightly carinate. Hypostomal lines only very slightly curved behind. Third antennal segment not knob-shaped, somewhat longer than in *Prionus* s. str., main sensillum small, flat, elongate oval. Mentum and submentum unpigmented. Palps unusually short,

first two segments of maxillary palps transverse, both maxillary and labial palps with very large apical sensory area. All prothoracic pigmentation extremely pale. In a single later instar larva, spiracles lack discernible marginal chambers; elongate, faintly pigmented. Anal tube not enlarged. Length of the available larva 55 mm.

Distribution: Central Asia.

Material: One later instar larva (coll. British Museum) labelled: »*Prionus brachypterus turkestanicus* SEM. The larva attacks roots of *Taraxacum koksaghyz* ROD. in Vrevskaia, Uzbekistan. 1936. Leg. and det. Shubin.« (B. M. number 1937-116.) See the commentary under *P. brachypterus.*

Prionus (Psilotarsus) brachypterus GEBLER, 1830

Larvae not available. Described by MAMAEV et DANILEVSKY (1975) according to three larvae which were at that time in collection of the Zoological Institute of Academy of Sciences of the USSR in Leningrad. According to M. L. Danilevsky, these larvae have disappeared from the collection. The description and illustrations agree well with the above described larva of *P. turkestanicus* (all the key characters hold), and as the larvae were even collected at the same locality (Vrevskaya, 28. 8. 1932, in soil on peanut plantation, lgt. D. Kolichek), they probably belong to the same species (*turkestanicus* has been earlier often considered as a subspecies of *brachypterus*). The determination of all the four above mentioned larvae remains uncertain till having a clear classification of the group, and till being sure about which of the species occurs in the above collecting spot (Vrevskaya, now Almazar). However, it could be presumed that larvae of all the species in the *brachypterus*-complex should be very similar to each other.

Prionus (*Polyarthron,* or *Microarthron*) *komarovi* DOHRN, 1885

Well distinguishable from other *Prionus*-larvae. Cranium slightly diverging posteriorly, deeply notched behind (Fig. 20F). Frontal lines enter antennal openings from below. Frons and gena very broadly and intensively pigmented. Frons moderately convex, finely rugose. Frontal carina low, mostly shallowly divided into three lobes on each side. Epistomal carina projecting far over clypeus, with broad triangular lateral angles and ± distinct medial pair of smaller teeth (sometimes even double). Labrum moderately long, oval to slightly cordate, with broad dark basal area and rather stout anterior setae. Gena at most moderately roundly protuberant. Posterior halves of hypostomal lines straight. Third antennal segment relatively large, cylindrical, at least as long as broad, main antennal sensillum extremely large, oval, protuberant (Fig. 20D). Labiomaxillary complex bearing comparatively sparse setae, but those of mala and particularly ligula are unusually strong. Mentum and submentum with pale yellow central area. Prothoracic pigmentation pale, indistinct. Spiracles very small, broad, faintly pigmented, marginal chambers absent. Pleural discs

extremely large (Fig. 21F). Anal tube remarkably enlarged (Fig. 19G). Large body areas, particularly very soft membraneous regions, distinctly roughly microreticulate. Body setae pale ferrugineous to almost unpigmented. Largest available larva 25 mm.

Host plants: *Haloxylon, Eremosparton flaccidum.* Development in roots, no more data available.

Distribution: Central Asia.

Material: 1972 and 1979 SU, Central Asia, Karakum, Repetek, 5/—, *Haloxylon* and *Eremosparton,* V. G. Kaplin lgt., coll. IS; 29. 4. 1973 SU, Turcmenia, Dzhilikum, 1/—, *Haloxylon,* B. M. Mamaev lgt., coll. IS. The larvae not reared, determined by elimination.

Genus *Dorysthenes* VIGORS, 1826

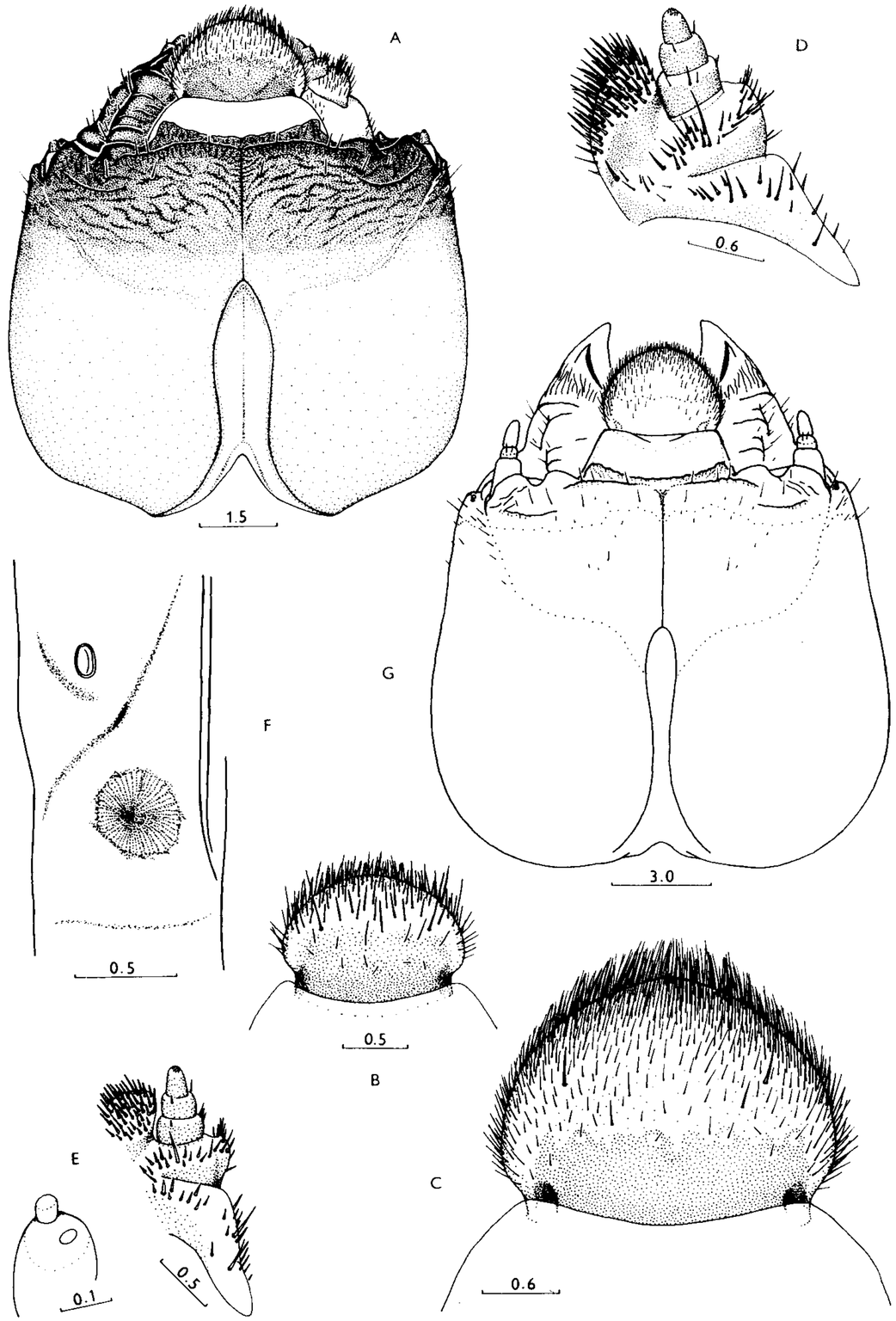
Dorysthenes (Cyrtognathus) paradoxus FALDERMANN, 1832

It has been found in a piece of wood at right bank of Ussuri-river representing the Soviet-Chinese border (LOBANOV, DANILEVSKY et MURZIN, 1981), therefore this species probably belongs to the fauna of the USSR. Larva not available, but at my disposal one larva of another *Dorysthenes*-species of the same subgenus, *D. (C.) hydropicus* PASCOE, 1857, which could be essentially similar. For a differential diagnosis of this larva see below. In addition to this, one larva of another subgenus available, namely *D. (Opisognathus) forficatus* (F., 1792) from Morocco, ex coll. British Museum. The larva is rather similar; it differs from *D. hydropicus* by rather bright pigmentation.

Dorysthenes (Cyrtognathus) hydropicus PASCOE, 1857

Cranium slightly diverging posteriorly, rather shallowly notched behind. Mouthframe moderately broadly pigmented, not very dark, pigmented area followed by remarkably pale transverse band. Frontal lines in later instar larva vanishing before antennal openings. Frons anteriorly slightly convex, very finely rugose. Frontal carina very low and blunt, without teeth. Epistomal carina short, blunt, smoothly emarginate. Labrum transverse, ± oval, with dense, short, stout anterior setae, hind half pigmented. Gena abruptly protuberant, almost carinate. Hypostomal lines almost not curved behind. Third antennal segment ± cylindrical, slightly longer than broad, main antennal sensillum small, flat. Labiomaxillary complex with dense, short, almost unpigmented setae, palpiger with abruptly prominent flattened lateral side,

Plate 21: A — *Prionus ?besicanus,* later instar, head, dorsal view (right mandible removed). B — *P. coriarius,* half-grown, labrum. C — *P. asiaticus,* submature, dtto. D — *P. coriarius,* mature, left distal maxilla, ventral view. E — *Dorysthenes hydropicus,* later instar, left distal maxilla, ventral view (right), and outline of apical part of right antenna, ventral view (left). F — *Prionus komarovi,* later instar, diagrammatic illustration of left epipleurum and spiracular area of first abdominal segment, showing very large pleural disc. G — *Callipogon relictus,* later instar, head, dorsal view.



its anterolateral angle bearing minute tubercle (Fig. 21E). Mentum and submentum unpigmented. Prothoracic pigmentation lacking. All spiracles with about ten very small yet relatively distinct marginal chambers. Femur and tibiotarsus with pigmented area restricted to lateral one-fourth. Anal tube not enlarged. All body setae unpigmented. Length 48 mm; according to DUFFY (1968) up to 75 mm.

Host plant: DUFFY (l.c.) lists *Saccharum officinarum* without any further data on habits. The larva probably feeds on underground parts of the plant.

Material: One later instar larva labelled China (ex coll. British Museum). According to Dr. Jane E. Marshall at the British Museum, this is one of the larvae described by DUFFY (l.c.), so that the following data are applicable to it: China, Taiwan, Tainan, Tsungyeh, from sugar estate, C. S. Wang lgt.

Supplement to *Prionus:* One indetermined damaged larva of *Prionus* differs from all other available species. It is characterized as follows: Cranium deeply notched behind, sides almost parallel. Frontal lines enter antennal openings from below. Mouthframe broadly heavily sclerotized. Frons rather flat, moderately relatively densely rugose, posterior transverse impression not very deep. Frontal carina moderately prominent, divided into three pairs of lobes, lateral one slender, tooth-shaped, medial two pairs broad. Epistomal carina projecting far over clypeus along whole width, shallowly divided into two broad lobes on each side. Six epistomal setae. Labrum moderately long, transversely oval, anterior half bearing relatively dense, short, stout setae. Gena rounded, subfossal process extremely long. Hypostomal lines ± straight. Third antennal segment cylindrical, hardly longer than broad, main sensillum very large, much larger than third segment's cross-section, flat. Labiomaxillary complex with short moderately dense setae, those on ligula very stout. Maxillary palpiger rounded laterally. Prothoracic pigmentation entirely lacking. Marginal chambers ± lacking. Legs poorly pigmented. Anal segment larger than in most other species, although not as large as in *P. komarovi*. Body setae very short, thin, sparse, on prothorax, however, rather dense. Length about 35 mm.

In addition to the above description, this larva differs quite sharply from all other available *Prionus*-larvae by extremely distinctly microsculptured dull body surface, particularly on the prothorax (other species may have pronotum ± rugose but always shining).

Material: SU, Tadzhikistan, Tigrovaya Balka, one larva in *Ferula,* lgt. D, coll. IS. The larva had a tunnel in the sand leading to a rotten *Ferula*-root, the larva found half inside it. Rearing failed, the larva was preserved in June 1978. Species unknown. Judging from some characters suggesting some affinity towards *Prionus komarovi* (large antennal sensillum, frontal carina, large anal tube, and, after all, the dull microsculptured body surface), the larva might belong to some species of the subgenus *Polyarthron*. No species known from the region to which the larva could be assigned.

Genus *Callipogon* SERVILLE, 1832
Subgenus *Eoxenus* SEMENOV, 1898

Type species: *Callipogon relictus* SEMENOV, 1898 (monobasic)

Body moderately elongate, with extremely short reddish setae which are more numerous on certain prothoracic regions.

Cranium (Fig. 21G) subquadrate (1.13), moderately depressed (1.93, one specimen measured), not microgranulate, hind half yellowish, mouthframe strongly sclerotized; epicranial halves very feebly convex laterally, with very short sparse anterior setae, fused almost along whole length, cranium only very shallowly emarginate posteriorly. Frontal lines ± distinct along whole length, narrow, strongly S--curved, narrowly entering antennal openings, not reaching anterior cranial margin. Frons short (shorter medially than dorsal duplicated region), transversely impressed at base, feebly convex anteriorly, at most finely transversely rugose. Anterior margin heavily sclerotized, pitchy, postcondylar carina short, low, frontal carina distinct, moderately prominent, obliterated about middle, not toothed, lateral ends distinctly longitudinally striate. Epistomal carina very sharp and prominent, laterally forming broad triangular plates, rather densely ± longitudinally rugose. Mostly six epistomal setae. Clypeus moderately broad, trapezoidal, feebly convex, at most pale yellowish. Labrum subcircular, with anterior and lateral margins broadly fringed with dense short reddish setae, two main discal setae in later instar larvae almost not differentiated from others. Basal half orange to ferrugineous, anterior half pale yellow. Discal sunken sensilla pigmented and very conspicuous. Anterior epipharyngeal region markedly sclerotized, separated from posterior raised portion by narrow transverse completely desclerotized zone; setae only on anterior region. Tormae feebly sclerotized, oblique, interrupted. Pleurostoma heavily sclerotized, with distinct vertical carina and prominent conical subfossal process. Gena dark ferrugineous, slightly wider than pleurostoma. Three pairs of main stemmata present, in mature larvae often rather small and broadly spaced, at least ventral two pairs facing anteriorly due to protuberant gena. Two dorsal stemmata on each side, in later instar larvae very small or indiscernible. Hypostomal lines distinct, pigmented almost along whole length, posterior half straight, reaching postoccipital line. Gula exposed, relatively broad yet distinctly narrower than one hypostomal sclerite. Metatentorial bridge in its narrowest region scarcely wider than gular bridge.

Antennae very long, two-segmented, connecting membrane large, antennae deeply retractile. Antennal ring distinctly projecting over connecting membrane, dorsal face rugose. Segment 1 cylindrical, bearing a few moderately long subapical setae. Segment 2 brightly pigmented, gently tapering, in later instar larvae about twice as long as broad, its apical unsclerotized area rather small, main sensillum very small, round or elliptical in apical view. Mandible with border zone markedly striate, apical part with three distinct long inner keels and one short curved carina

at dorsal angle (once delimiting inner striated plate which is here absent). Dorsal face of apical part with one abrupt curved ridge. Basal part relatively smooth, often sparsely transversely striate, with greater number of short lateral setae, molar portion glabrous. Labiomaxillary complex very robust, with its scattered sunken sensilla unusually distinct, dark pigmented. Submentum strongly sclerotized, with a few (mostly two) discal setae. Connecting lobe densely setose, its medial face with pigmented spot. Cardo may bear a few minute setae on posterior face. Stipes with basal pigmented band ± complete, laterally very pale. Palpiger with numerous setae, process absent. Mala short, robust, cylindrical, bearing extremely dense short stout setae, inner face not broadened and carinate (Fig. 22A). Maxillary palp relatively short, robust, segments decreasing in length from 1 to 3, third segment strongly tapering, apical sensory area small. Mentum ± separated from submentum by shallow somewhat darkened impression; central area sclerotized, anterior angles densely setose. Pigmentation of labial palpigers ± connected, palps short, first segment in later instar larvae with rather numerous setae on apical unsclerotized margin, second segment abruptly tapering. Ligula broad, with slightly sclerotized basal spots along sides, covered with extremely dense very short setae. Hypopharyngeal notch very distinct, anterior dorsal labial portion extremely short (much shorter than in *Ergates,* cf. Fig. 18C), posterior portion completely devoid of setae.

Prothorax with dorsal pigmented band and pigmented areas of epipleurum and lateropraesternum yellow-orange, almost continuous, not spotted. Anterior margin before dorsal pigmented band beset with remarkably numerous very short setae. Pronotum finely distinctly rugose, medial line slightly impressed anteriorly. Sublateral impressions distinct, very short, triangular, followed by narrow oblique impressed line. Alar lobes overall sclerotized. Posterodorsal epipleural angle separated, but not fused with alar lobe. Praesternum covered with rather dense, very short setae. Mediopraesternum not defined anteriorly, with distinct broad medial impression at hind margin. Episternum sclerotized and pigmented, with longitudinal unpigmented protuberance. Pleural sulcus S-curved, without lateral fovea. Mediopraesternum expanded backwards, remarkably quadrangular posteriorly and much reducing medial portions of coxosternal halves which are very small and broadly separate.

Meso- and metathoracic scuta laterally with very fine yet in later instar larvae well discernible anterior microscopic spines. Postnotal fold well developed, metascutum uninterrupted (lines not X-shaped), scutum I very poorly defined even on metathorax. Mesothoracic spiracle slightly protruding into prothorax, moderately large (cf. *Megopis*), most of its hind margin with many very narrow marginal chambers. Rudimentary metathoracic spiracle distinct. Some ventral regions (e.g. pleurum) may bear inconspicuous microscopic spines. Transsternal lines and lines dividing basisternum very sharp and distinct.

Legs slightly longer than maxillary palps. Trochanter complete, distinct, with several medial setae. Tibiotarsus slightly longer than femur, both laterally pigmented

and bearing numerous medial setae. Praetarsus slender, acutely conical, rarely with minute seta, apical portion mostly pigmented.

Typical Prionine ambulatory ampullae, densely finely rugose, microscopic spines almost absent. First abdominal spiracle slightly larger than remaining ones, its length about 0.4 (at most 0.5) of that of mesothoracic spiracle. Abdominal spiracles rather broadly oval, with almost whole their hind margin bearing numerous narrow marginal chambers. Large pleural disc (just slightly smaller than its spiracle) on segment 1, remaining discs small and decreasing in size from segment 2 to 6. Ninth segment much longer than eighth, anal segment finely separate, anus terminal but distinctly moved dorsad, anal papillae normal, dorsal one not enlarged, all three with only very sparse short setae. Length up to about 150 mm, largest available larva 120 mm.

One species of this (generally Neotropical) genus occurs in the Ussuri-region and Korea. It has been described in a separate subgenus *Eoxenus* SEMENOV, 1898. However, some authors classify this species in *Callipogon* s. str. The larva is quite dissimilar to *Ergates,* and including *Callipogon* in Ergatini is not correct.

Callipogon (Eoxenus) relictus SEMENOV, 1898

Host plants: Apparently polyphagous on deciduous trees. Known food plants include *Ulmus, Betula, Tilia, Fraxinus, Populus, Quercus, Acer.* According to LYUBARSKY (1953), the larvae live in the wood of dead stems of great diameter, standing or fallen, often infested with the fungus of the genus *Pleurotus.* Three-year life-cycle. Pupation in spring, flight period long - late July to early September. According to CHEREPANOV (1979), development period of at least five years.

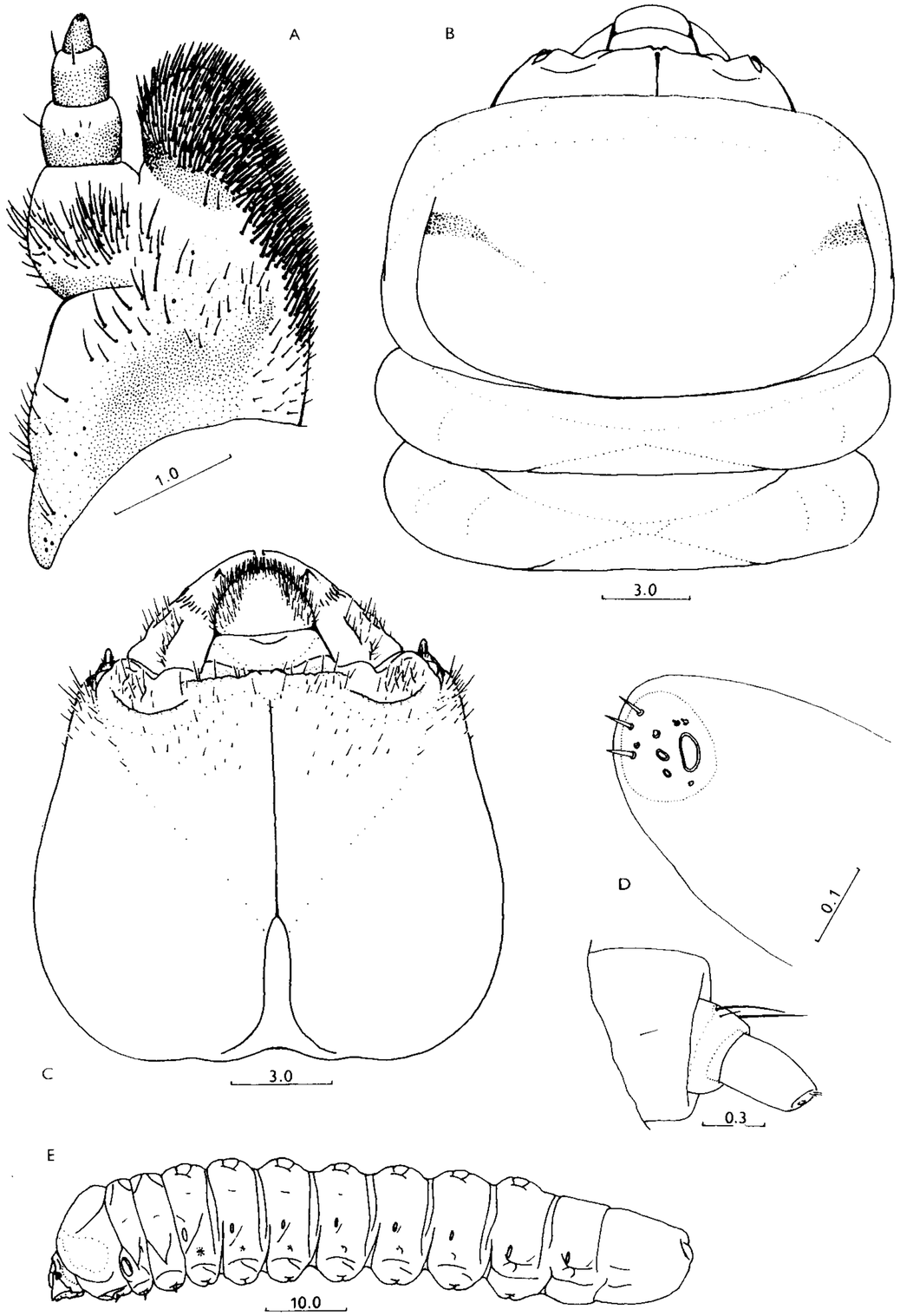
Material: 20. 5. 1976 SU, Bychikha, 1/I, *Betula,* A. V. Kompantsev lgt., coll. IS; 17. 4. 1969 SU, Suputinka Nature Reserve, 3/I, *Betula* and *Ulmus,* B. M. Mamaev lgt., coll. IS.

Genus *Rhesus* MOTSCHULSKY, 1838

Type species: *Rhesus serricollis* MOTSCHULSKY, 1838 (monobasic)

Body elongate, with short rusty brown setae.

Cranium subquadrate (1.1—1.2), moderately depressed (1.8—2.0), particularly mouthframe distinctly very finely microgranulate, dull; anteriorly yellowish, posteriorly almost unpigmented, mouthframe heavily sclerotized, dark ferrugineous to pitchy. Cranium slightly diverging, widest posteriorly. Epicranial halves with relatively numerous anterior setae, fused along whole length, cranium with only very shallow posterior emergination. Frontal lines very inconspicuous, almost straight, ending blindly before antennal openings. Frons very long (Fig. 22C), much longer medially than dorsal duplicated region (exact proportion somewhat variable); ± smooth, feebly convex anteriorly, with rather numerous short to miniature setae in anterior exposed region. Postcondylar carina long, distinct, with relatively blunt



edge. Frontal carina distinct, moderately prominent, narrowly medially interrupted, medial end of each half usually with small tooth. Epistomal carina blunt in middle, laterally projecting far over clypeus as two large ± triangular plates. Often more than six epistomal setae. Clypeus narrow, feebly convex, with yellow to orange pigmentation at base and along sides. Labrum subcircular to cordate, base and central region sclerotized, broad anterolateral margin pale. Labrum broadly fringed with rather long setae, in later instar larvae main discal pair not recognizable. Epipharynx unsclerotized, setae reaching far behind along whole posterior raised portion. Tormae broad, long, slightly angulate, with short anteromedial branches; reaching about as far behind as setal rows. Pleurostoma strongly sclerotized, very dark, with distinct vertical carina. Subfossal process conical, of varying size, in later instar larvae often large. Gena almost smooth, pigmentation usually somewhat narrower than pleurostoma. Three (rarely only two) very small variable main stemmata on each side, other stemmata absent. Hypostomal lines distinct, at most gently curved posteriorly, reaching postoccipital line, pigmented in anterior two-thirds. Hypostomal sclerites often bearing several minute setae. Gular bridge extremely narrow, gula entirely covered, much narrower than one hypostomal sclerite. Metatentorial bridge twice or more than twice as broad as gular bridge.

Antennae relatively long, deeply retractile, two-segmented (Fig. 22D). Antennal ring uninterrupted, its dorsomedial portion projecting far over connecting membrane, dorsal face in later instar larvae roughly irregularly rugose. Segments strongly sclerotized, segment 1 with several long dorsal subapical setae, segment 2 slightly to almost twice longer than broad, gently tapering, obliquely truncate apically, terminal unsclerotized area small, main sensillum small, flat, elliptical. Particularly outer mandibular surface very finely microsculptured, dull. Border zone indistinctly striate. Apex prominent, dorsal angle reduced, blunt. Three distinct inner keels, inner striated plate feebly developed. Cutting edge rather blunt, running from apex distinctly not to dorsal angle but dorsad above it (Fig. 23A). Dorsal plate with only two to three coarse blunt ridges. Basal portion not remarkably sculptured, with great number of lateral setae, dorsal face of molar portion bearing small group of short setae. Labiomaxillary complex with unusually thin setae (some of them rather long) which are, however, much stronger on ligula and mala. Submentum sclerotized, with two stronger and mostly some small setae, main pair not shifted to anterior border. Connecting lobe unsclerotized, with numerous setae. Stipes with basal band complete but its lateral extremity very narrow due to large pale area. Palpiger process absent. Segments of maxillary palps shortening from 1 to 3. Segment

Plate 22: A — *Callipogon relictus,* submature, right distal maxilla, ventral view. B — *Rhesus serricollis,* later instar, outline of head and thorax, dorsal view. C — *R. serricollis,* submature, head, dorsal view. D — *R. serricollis,* submature, right antenna with connecting membrane, lateral view (lower), and apical part of second segment, ventral view (upper). E — *R. serricollis,* later instar larva, lateral view. (Setae not figured.)

1 extremely broad, third segment moderately robust, apical sensory area small. Mala moderately broad, inner face sharply carinate. Mentum separated from submentum, darkened along this border, central area sclerotized, yellow to orange. Labial palps short, first segment broad, mostly with at least one seta on distal margin, second segment rather slender. Ligula broad, ± without basal sclerotization, hypopharyngeal notch distinct, anterior dorsal labial portion long, both anterior and posterior portions with numerous setae.

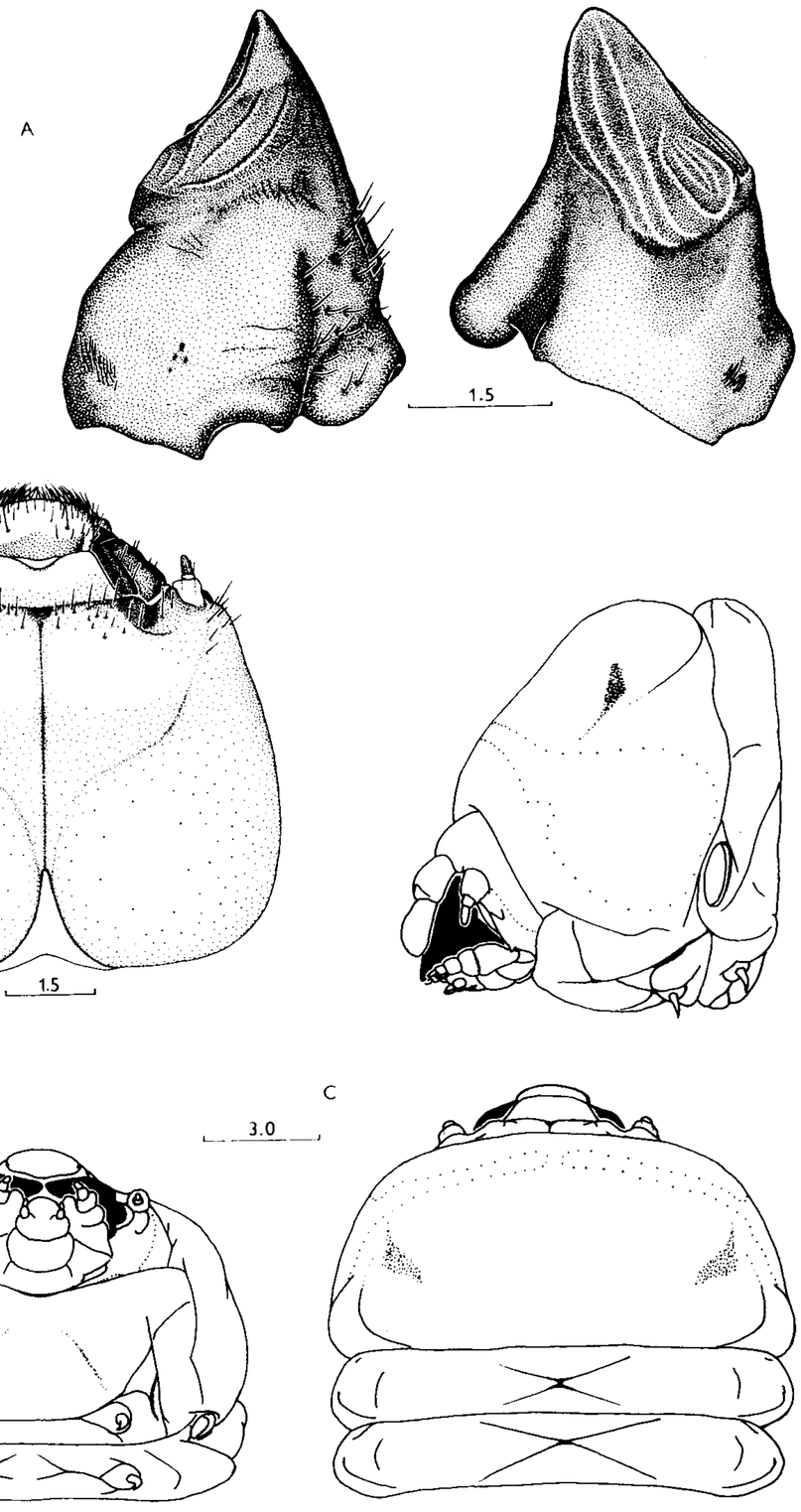
Prothorax with pigmented areas distinct, yellow-orange, homogeneous, not spotted, particularly that of lateropraesternum very bright and distinct. Pronotum finely irregularly rugose, medial line almost not impressed, lateral furrows distinct, sublateral impressions broad at base, oblique, abruptly tapering, turn into narrow impressed lines. Epipleurum entire, its posterodorsal angle not fused with alar lobe. Episternum moderately sclerotized, with distinct longitudinal protuberance. Pleural sulcus strongly S-curved, with deeply impressed lateral fovea. Mediopraesternum almost not delimited anteriorly, expanded and quadrangular posteriorly, both halves of coxosternum much reduced, small, broadly separate.

Meso- and metanotum in later instars not microspiculate, dull, microreticulate. Postnotal fold feebly developed (Fig. 22B), distinctly associated with mesothorax. Metascutum uninterrupted. Scutum I defined on metathorax. Mesothoracic spiracle very distinctly protruding into prothorax, extremely large (in young larvae about twice, in mature larvae about four times as long as maxillary palp), hind margin (and sometimes upper section of anterior margin as well) with very numerous extremely small marginal chambers. Metathoracic spiracle indiscernible. Transsternal lines sharp, oblique lines on basisternum present.

Legs very short, about as long as maxillary palp. Trochanter very short yet complete, with several setae. Femur transverse, both femur and tibiotarsus laterally pigmented, bearing numerous stout setae. Praetarsus conical, slender, its tip pigmented.

Typical Prionine ampullae, finely rugose, not microspiculate. Spiracles very large (Fig. 22E), with many very smal marginal chambers along hind margin. First spiracle much larger than remaining ones, about 0.6 of mesothoracic spiracle length. Pleural disc 1 large and distinct, discs 2 to 6 much smaller. Segment 9 very long (about 1.5 times as long as 8), broadly rounded posteriorly, anus pronouncedly posterodorsal, anal segment fused with segment 9 (Fig. 22E), anal papillae distinct, large, bearing scattered short setae. Length up to 95 mm.

Plate 23: A — *Rhesus serricollis,* submature, right mandible, dorsal (left) and medial (right) views. B — *Macrotoma scutellaris,* mature, head, dorsal view. C — *M. scutellaris,* later instar, outline of head, pro-, meso- and (in dorsal view) metathorax, dorsal (lower right), lateral (upper right) and ventral (left) views. (Note non-developed postnotal fold and divided prothoracic epipleurum.)



This genus is represented by only one Palaearctic species, however, it has close relatives in Australasian Region (limited material of non-Palaearctic Prioninae available to me at the moment, but e.g. the larva of *Agrianome spinicollis* is so similar that it must be considered congeneric with *Rhesus*).

Rhesus serricollis MOTSCHULSKY, 1838

Host plants: Available larval material has been taken from *Fagus, Celtis* and *Platanus*. Apparently polyphagous on deciduous trees of sufficient diameter. Larvae live in rotten wood of large trunks, both standing and fallen. At least three-year life-cycle. Pupation in the wood. Emergence of adults in late summer; they are night-active, often hidden in their emergence holes during the day.

Distribution: Caucasus, Transcaucasia, North Iran, Asia Minor, Syria, in Europe reaching SE Bulgaria.

Material: Turkey, Alanya, one larva from *Platanus* sp., P. Schurmann lgt., coll. M. Sláma; 27. 8. 1976 Bulgaria, Ropotamo, Arkutino, 8/I, *Celtis australis*, lgt. et coll. S; 13. 8. 1966 SU, Krasnodar region, Krasnaya Polyana, 3/I, *Fagus*, B. M. Mamaev lgt., coll. IS.

Genus *Macrotoma* SERVILLE, 1832
Subgenus *Prinobius* MULSANT, 1842

Type species: *Prinobius myardi* MULSANT, 1842 = *Prionus scutellaris* GERMAR, 1817 (?monobasic)

Body short, robust, with fine ± ferrugineous setae.

Cranium slightly transverse (1.2–1.3), moderately depressed (about 1.9), not conspicuously microgranulate, very pale, mouthframe weakly sclerotized (Fig. 23B). Sides almost not convex, slightly diverging posteriorly, cranium somewhat trapezoidal. Each epicranial half with very few thin anterior setae, both halves fused almost along their whole length, cranium very shallowly emarginate posteriorly. Frons extremely long, its hind angle extended far backward; about three times as long in middle as dorsal duplicated cranial region. Frontal lines poorly visible, strongly S-curved, ending blindly near antennal openings. Frons almost smooth, its hind half broadly impressed, anterior half convex, bearing in front some thin, short setae. Postcondylar and frontal carinae in younger larvae absent, in mature larvae rudiments present. Epistomal carina absent. Anterior frontal margin almost unpigmented except for small antennal shell, large dark spots at dorsal mandibular articulations and medial dark triangular spot at anterior extremity of medial frontal line. Often more than six epistomal setae, sometimes not sharply separated from other frontal setae due to absence of frontal carina. Clypeus relatively narrow and long, feebly convex, moderately tapering, with straight sides. Basal half yellowish to orange, anterior margin shallowly emarginate. Labrum transverse, of characteristic shape - - sides diverging anteriorly, front margin broadly rounded to somewhat cut. Basal half pigmented, several scattered discal and lateral setae present, anterior margin,

however, bearing extremely dense rather long and thin reddish setae (they are particularly dense in mature larvae in which ± divided into many separate tufts). Epipharynx almost unsclerotized, anterior areas of very dense short setae projecting backwards as narrow sparse rows along almost whole hind raised portion. Tormae broad, strongly sclerotized, unbroken, running abruptly obliquely backwards, reaching about to posterior extremities of setal rows. Pleurostoma ferrugineous to dark brown, only upper part raised, lower part rather smooth and flat. Subfossal process very short, blunt, indistinct, in young larvae absent. Gena intensively but narrowly pigmented, narrower than pleurostoma, then any pigmentation abruptly disappears. Stemmata ± absent (there are often various rudiments of main stemmata, but always very obscure). Hypostomal lines distinct, S-curved, vanishing just before postoccipital line, only very short anterior sections pigmented. Gula very narrow (more than twice narrower than one hypostomal sclerite), entirely covered, postgular lobe finely sclerotized. Metatentorial bridge slightly less than twice as broad as gular bridge.

Antennae very long, two-segmented, deeply retractile, connecting membrane very large. Very small medial antennal shell present, connecting membrane almost entirely visible from above, in young larvae antennal shell absent. Segment 1 with several long subapical setae, segment 2 brightly pigmented, slightly tapering, much longer than broad (occasionally more than twice as long as broad), obliquely cut apically, terminal unsclerotized area small, main sensillum small, flat, subcircular. Mandibles very short and robust. Only short outer section of border zone striate. Apex acute, prominent, dorsal angle blunt, reduced, both connected by simple continuous cutting edge. Three long inner keels and one short below dorsal angle, inner striated plate absent. Two low ridges in place of dorsal plate. Lateral face of basal portion uneven, with moderately numerous short setae, other surface smooth, shining, dorsal side of molar portion in some individuals bearing small group of short setae. Labiomaxillary complex robust, with relatively sparse setae (rather dense on ligula and mala). Submentum poorly sclerotized, main two setae only slightly shifted to anterior border, other setae at most very small. Connecting lobes unsclerotized, with 15–20 setae each in later instar larvae. Stipes with complete pigmented band, its lateral extremity very narrow. Palpiger process absent. Segments of maxillary palp abruptly shortening from 1 to 3, first segment extremely broad, third very small, apical sensory area moderately large. Mala rather narrow, inner side very feebly carinate. Mentum well separate from submentum, at most finely sclerotized, pale yellowish, basal sclerotization absent. Pigmentation of labial palpigers ± connected (not, however, in exuviae in which medial connecting spot disappears). Labial palps short, segment 1 broad, with dorsal tuft of several setae on apical margin (may be reduced or lacking in young larvae), segment 2 very small. Ligula broad, with basal sclerotized spots, hypopharyngeal notch indistinct, anterior dorsal labial portion long, covered with dense short reddish setae, limited number of setae also present on posterior portion.

Dorsal prothoracic band pale, yellow, epipleurum and lateropraesternum almost unpigmented. Pronotum very large, abruptly obliquely inclined, finely irregularly rugose, hind margin longitudinally striate, medial line not impressed. Lateral furrows short, not reaching pigmented band, sublateral impressions very short, broadly triangular. Posterodorsal epipleural angle not fused with alar lobe, rather suppressed by mesothoracic spiracle. Epipleurum with very distinct ± transverse sharply impressed line in anterior half (Fig. 23C, absent in all preceding genera). Mediopraesternum poorly delimited at apex, even lateral limits not very distinct, posterior region expanded, quadrangular, much reducing and broadly separating coxosternal halves. Pleural sulcus strongly S-curved, with deeply impressed fovea at lateral extremity. Episternum at most finely pigmented, without protuberance.

Meso- and metanotum in later instar larvae without microscopic spines, both divided by not very distinct X-shaped lines, postnotal fold non-developed. Scutum I inconspicuous. Mesothoracic spiracle protruding strongly into prothorax, moderately large (at most twice as long as maxillary palp in later instar larvae), oval, marginal chambers absent. Metathoracic spiracle indiscernible. Transsternal lines distinct, oblique lines on basisterna obscure.

Legs very short, shorter than maxillary palps, very robust. Trochanter much reduced, developed in form of very narrow ring. Femur transverse, tibiotarsus scarcely longer than femur, about as long as broad, both segments laterally pigmented and bearing very dense medial setae. Praetarsus about as long as tibiotarsus, setae absent, apex slender, sclerotized.

Typical Prionine ambulatory ampullae, almost smooth, in later instars without microscopic spines. First abdominal spiracle almost not larger than remaining ones, slightly less than twice shorter than mesothoracic spiracle. Marginal chambers absent. Small rather indistinct pleural discs may be found on all six anterior abdominal segments. Ninth segment remarkably longer than eighth. Anus terminal, anal segment finely separate from segment 9, anal papillae distinct, dorsal one not enlarged, all bearing short scattered setae. Length up to 50 mm.

One species at my disposal:

Macrotoma (Prinobius) scutellaris (GERMAR, 1817)

Host plants: Available larvae taken from *Quercus, Pirus* and *Acer,* probably polyphagous on many deciduous trees. According to M. Sláma (personal communication), larvae feed in rotting wood of dead stems, both standing and fallen, with at least little moisture. Several-year development, pupation in the wood in spring/summer, flight in summer.

Distribution: Mediterranean area (incl. North Africa), Crimea, Caucasus, NW Iran.

Material: June 1981 and 1982 Greece, Creta, Omalos, 4/I, *Quercus,* M. Sláma lgt. et coll; June 1984, same locality, 1/—, *Pirus,* J. Kratochvíl lgt., coll. S; June 1969 France, Alpes Maritimes, Le Muy, 4/I, *Quercus,* M. Sláma lgt. et coll; Italy, Gargano, M. Sacro, 1/—, *Acer,* G. Sama lgt., coll. S.

Subfamily Necydalinae LATREILLE, 1825

General morphology

Body white or yellowish, moderately elongate, almost not depressed, tapering posteriorly, with extremely short moderately dense ferrugineous setae.

Head in natural position about by half retracted. Cranium narrower than prothorax, moderately transverse and depressed, relatively pale, at most yellow, mouthframe strongly sclerotized; relatively numerous very short anterior setae (Fig. 24A). Sides moderately roundly convex, both epicranial halves shortly fused, the doubled epicranial region anteriorly usually slightly raised and projecting above hind frontal angle. Frons triangular, frontal lines rather indistinct, slightly S-curved, passing through lateroventral portions of very large antennal openings, reaching very distinctly anterior cranial margin. Almost no remains of the original incurved frontal sutures, transfrontal line absent. Postcondylar carinae absent. Epistomal margin simple, not keeled, abruptly raised above clypeal level. Mostly six epistomal setae. Medial frontal line ± entire, reaching epistomal margin. Clypeus and labrum small. Clypeus trapezoidal, filling the entire space between dorsal mandibular articulations, devoid of setae. Labrum slightly narrower than clypeus, moderately transverse, at least basal half sclerotized, anterior margin densely setose. Epipharynx bearing ± numerous anterior setae, its hind portion very narrow, strongly raised, tormae broad, long, curved backwards and running along sides of the hind portion. Pleurostoma broad, moderately raised, deeply sclerotized, subfossal process absent, or a very low broad tubercle present. Gena narrowly sclerotized. One to three small flat or at most feebly convex main stemmata on each side, occasionally almost indiscernible, other stemmata absent. Hypostomal lines parallel or slightly converging backwards, may or may not reach postoccipital lines. Anterior margin of ventral sclerite sharply separate from the base of labiomaxillary complex, hypostomal portion of that margin sclerotized. Metatentorial pits very small and close to hind margin, metatentorial arms slender, connected by a very narrow bridge, pointed obliquely inwards, poorly visible in ventral view, occipital foramen does not seem to be divided. Gula long, gular lines ± abruptly raised, medial gular line non-developed (at most a diffuse medial brightening). Both the gular and particularly the hypostomal regions bearing ± numerous short setae.

Antennae three-segmented, long, very deeply retractile, connecting membrane very large. Segments 1 and 2 elongate, the second segment up to twice longer than broad, segment 3 at most slightly longer than broad. Main antennal sensillum small, conical, situated ventrally in regard to the third segment. Mandible short, very robust, all transitions between the types I and II occur (Figs 24G to I). Apical part with three long inner keels reaching apex. Border zone striate and/or roughened. Basal portion bearing two or more short lateral setae. Labiomaxillary complex robust, individual basal components well separate. Cardo large, free, movable.

Stipes with broad basal pigmented band, maxillary palpiger of varying size, palp three-segmented, short, stout, both palpiger and the first palpal joint without process. Mala very broad to relatively narrow (Figs 24D, E), densely setose, with distinct oblique pigmented band. Mentum with ± distinct separate basal spots, pigmentation of both labial palpigers separate, palps short, moderately to very robust (Figs. 24D to F), ligula bearing sparse ventral and apical setae and relatively distinct dorsal marginal microtrichia, and usually with ventral pigmented spot.

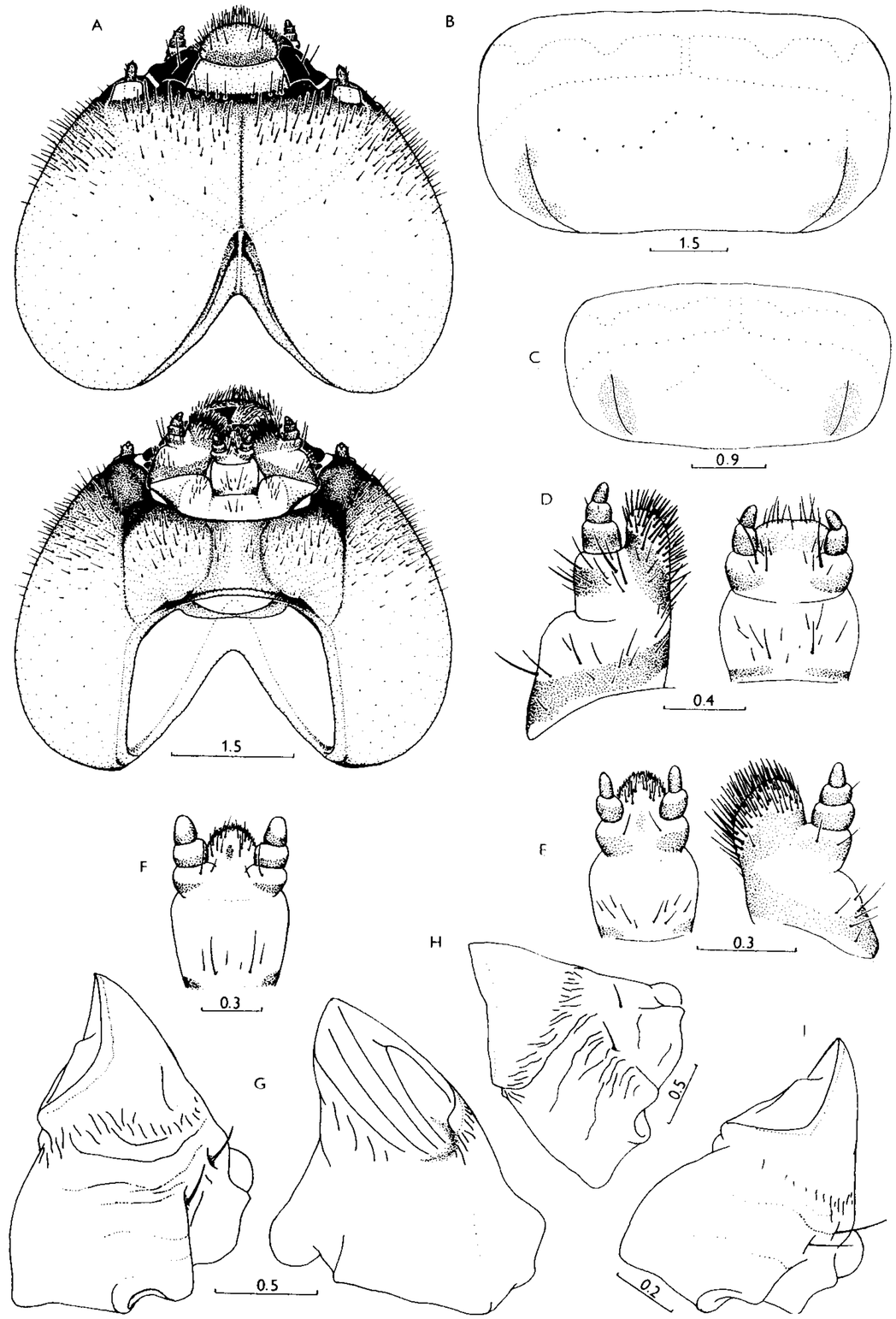
Prothorax robust, ± distinctly widest of body segments. Lateral furrows distinct in hind half of the pronotum, do not interrupt the anterior pigmented band, the latter occasionally very indistinct or almost absent, with two not very distinct anterior notches on each side. Pronotum bearing numerous scattered setae. Epipleurum and all ventral parts well defined, no fusions or modifications occur. All these regions (excepting epimeron) largely ± finely microspiculate, including the lateropraesternum (which is always smooth in the Lepturinae, except for the anterior margin). CRAIGHEAD's (1923) data about some North American species lacking these spines on the lateropraesternum are apparently incorrect - see LEECH (1966) who found them present in *Necydalis cavipennis* LECONTE, contrary to CRAIGHEAD (l. c.). Mediopraesternum triangular, bearing greater number of setae, lateropraesternum densely setose.

Meso- and metanotum non-granulate, entirely microspiculate, divided by X-shaped lines (occasionally very indistinct). Postnotum non-developed. Scutum I poorly defined. Alar lobes almost not protuberant. Mesothoracic spiracle lying on epipleurum-alar lobe border, not protruding into prothorax, oval, with some small marginal chambers. Rudimentary metathoracic spiracle at most very indistinct. Coxae almost not defined, fusing with the neighbouring areas. Transsternal line present, often not very distinct, basisternum may be divided. Sternum ± microspiculate, may be granulate *(Necydalis)*.

Legs (Fig. 25B) short, stout, all segments distinct. Praetarsus ± acutely conical, sclerotized apically, bearing one seta from inner side.

Abdomen with ambulatory ampullae on segments 1 to 7, the seventh ampulla ± reduced. Ampullae largely microspiculate, in *Necydalis* they are granulate (Fig. 25C). Dorsal ampullae with two broadly separate lateral impressions on each side (corresponding with main retractor muscles divided in two separate streams), the lateral one of these impressions on posterior ampullae moved strongly towards sides, almost pushed off from the ampulla. The medial pair connected by one incomplete transverse line. Parascutum poorly separate from spiracular area, spiracles

Plate 24: A — *Necydalis maior*, mature, head, dorsal (upper) and ventral (lower) views. B — *N. maior*, mature, diagrammatic illustration of prothorax, dorsal view. C — *N. pennata*, later instar, dtto. D — *Ulochaetes leoninus*, later instar, distal labium (right) and distal right maxilla (left), ventral view. E — *Necydalis morio*, later instar, distal labium (left) and distal left maxilla (right), ventral view. F — *N. maior*, mature, distal labium, ventral view. G — *N. maior*, mature, right mandible, laterodorsal and slightly apical (left) and medial (right) views. H — *N. ulmi*, mature, right mandible, laterodorsal and slightly apical view. I — *N. morio*, later instar, dtto.



bearing marginal chambers. Epipleurum distinctly protuberant at least on segments 6 to 9, but even then on the other segments ± defined and may become protuberant in contracted larvae. Pleural tubercles almost not defined, pleural discs absent. Pleural lobe separated by an oblique line, may be ± completely fused with the epipleural fold, poorly defined on segments with the latter fold not distinctly protuberant. Lateral impressions of ventral ampullae long, distinct, but the transsternal line shortened, not reaching the latter impressions, terminated by another pair of short impressions. Caudal armature absent, but some very large specimens of *Necydalis* may have a very fine ± paired pigmented spot at hind margin of the ninth tergum. Anal tube subterminal, simple, moderately large, anus triradiate, anal papillae well separate, bearing short setae.

The above description based on larvae of the only Holarctic genera, namely *Necydalis* L., 1758, and *Ulochaetes* LeConte, 1854. Larvae of both these genera available to me, *Necydalis* represented by several Palaearctic species, *Ulochaetes* - by its single species *U. leoninus* LeConte, 1854. The two genera differ mainly by the following characters:

1(2) Maxillary palpiger small, mala very broad (Fig. 24E). Prothoracic tergum with microscopic spines usually restricted to small areas along lateral furrows (Figs 24B, C), in any case pronotum never with whole hind half microspiculate. Pterothoracic sterna and ambulatory ampullae granulate (Fig. 25C), granules smooth . . . . . *Necydalis*

2(1) Maxillary palpiger large, mala narrow, ± cylindrical (Fig. 24D). Pronotum behind anterior pigmented band entirely microspiculate. Pterothoracic sterna and ambulatory ampullae non-granulate, continuously microspiculate . . . . . *Ulochaetes*

Other genera of Necydalinae occur only in the Neotropical Region, their larvae unknown.

Distribution: Necydalinae occur in Palaearctic, Oriental, Nearctic and Neotropical Realms. The Old World harbours only species of the genus *Necydalis*.

Habits of Necydalinae, when known, apparently similar. Larvae feed in the wood of dead standing trees, or in dead parts of living trees (hollows etc.), in stems or root bases. More rarely found in fallen trees. Several-year development, pupation in spring-summer in the wood, flight in summer, adults do not visit flowers.

Genus *Necydalis* L., 1758

Type species: *Necydalis maior* L., 1758

Linsley et Chemsak (1972) were uncertain as to the proper type species. Some authors give *Necydalis maior* without further explanations. Even if it was found that *Necydalis* (now *Molorchus*) *minor* L., 1758, was the first designated type species (perhaps by Westwood, 1840), I am sure that the designation would be invalidated by the International Comission on Zoological Nomenclature, as the necessary outflowing changes would be, in my opinion, unacceptable, and in sharp contradiction to the stability principle.

Cranium (Fig. 24A) moderately transverse (about 1.4), very feebly depressed (1.8–2.0), at most very pale yellowish. Labrum transversely oval, often finely sclerotized also in anterior half except for narrow marginal region, very few (often two) discal setae present. One (very rarely two) main stemmata on each side, may be almost indiscernible. Ventral sclerite moderately long (about 3.0–4.5). Antennae very long, second segment up to twice as long as broad (in some specimens even slightly more than twice). Mandible with two lateral setae, type II-keel in some species very much reduced or absent. Maxillary palpiger small, mala not apparently borne on palpiger, broad, much broader than maxillary palp, in some species right and left mala almost touching above reduced ligula when maxillae are closed. Labial palps often pointed obliquely ventrad, ligula narrow, usually with distinct elongate pigmented spot (Figs 24E, F).

Prothoracic pigmented band pale, occasionally almost absent. Protergum with microscopic spines restricted to small areas along lateral furrows (perhaps more widespread in *N. ulmi*). Spiracles with very small marginal chambers. Pterothoracic sterna and ambulatory ampullae granulate (in some species granulation slightly more restricted than in *N. maior,* Fig. 25C). Epipleurum of several anterior abdominal segments feebly protuberant, particularly in *N. maior*.

Larvae of four species available:

1(4) Labial palps ± stout, apical sensory area large and facing ± distinctly ventrad (Fig. 24F). Mandibular type II-keel much reduced (Fig. 24G).

2(3) Larvae more sclerotized. Cranial setae distinctly reddish, stemma ± surrounded by pigmentation, epistomal margin almost equally broadly sclerotized along whole width, labrum pigmented at least in basal half . . . . . *maior*

3(2) Larvae very poorly sclerotized. Cranial setae almost unpigmented, pigmentation behind stemmata lacking or extremely indistinct, epistomal margin narrowly sclerotized except for larger spots at medial frontal line and dorsal mandibular articulations, labrum very poorly pigmented except for narrow basal band. Far East islands . . . . . *gigantea*

4(1) Labial palps slender, apical sensory area not remarkably large and ± terminal (Fig. 24E). Type II-keel large (Fig. 24I) . . . . . *morio, pennata*

Necydalis ulmi has been described from a single exuvia (see below), and has not been included in the key*). In additon to the above five species, larvae of two Japanese species at my disposal: *N. harmandi* Pic, 1901, and *N. odai* Hayashi, 1951.

Necydalis maior L. 1758

Main stemma usually relatively distinct, ± convex, surrounded with pigmented cuticle. Third antennal segment slender. Mandible with type II-keel much reduced.

*) Note added in proof: In the meantime, one half-grown larva of *N. ulmi* could be studied (1985 CS, Slovakia or., Rem. Hámre, 1/I, *Fagus,* lgt. J. Hála, coll. S). Characters observed on the exuvia have been ± confirmed. Larva similar to *N. maior*. Pigmentation of mouthframe less intensive and ± narrower, one main stemma on each side, cuticle behind it at most very finely pigmented. Mandibular type II-keel extremely reduced (it would be probably ± lost in mature larva). Differs from all other *Necydalis*-species known to me by having a broad transverse band of very distinct microscopic spines along whole pronotal base.

Mala in later instars very broad, praelabium very characteristic (Fig. 24F). Prothorax with most of microscopic spines along lateral furrows found on alar lobes (Fig. 24B). Length up to 25 (−40) mm.

Host plants: Larvae in many deciduous trees, e.g. *Quercus, Carpinus, Betula, Alnus, Salix, Populus, Tilia, Fraxinus* etc. I have always collected the larvae in ± decaying material, never in sound wood.

Distribution: Temperate Palaearctics from Europe to Far East, perhaps also in Japan (*Necydalis aino* KUSAMA).

Material: 1963−84 CS, Bohemia, various spots, +/I, *Carpinus, Alnus, Tilia, Betula,* lgt. et coll. M. Sláma and S; 9. 7. 1969 France, Hautes Alpes, Pelvoux, 1/I, M. Sláma lgt. et coll; 2. 9. 1975 SU, Khabarovsk region, Gur, 3/I, *Betula,* lgt. D, coll. IS; 28. 5. 1975 SU, Amur region, Kundur, 3/I, *Betula,* lgt. D, coll. IS.

Necydalis gigantea KANO, 1933

Generally similar to *N. maior,* but many characters (micr. spines on protergum, antennae, poor sclerotization) somewhat transitional towards *pennata* and *morio.* However, the type II-keel of mandibles even more reduced than in *N. maior,* although in available larvae never completely lacking as in *N. ulmi.* Only non-mature larvae available.

Host plants: *Morus bombycis* (NAKAMURA, 1981). Other bionomical data published by Japanese authors in Japanese.

Distribution: Japan, listed by some Japanese authors (e.g. HAYASHI, 1980) for the Kurile Islands.

Material: Japan, four larvae with no data, coll. S. Nakamura.

Necydalis ulmi CHEVROLAT, 1838

One single incomplete exuvia available. Larva apparently similar to *N. maior.* Sclerotization of epistomal margin slightly narrower than in most specimens of *N. maior.* Main stemmata distinct (the available larva with one left stemma but two main stemmata on the right side), not entirely surrounded by distinctly pigmented cuticle. Third antennal segment small. Mala very broad, praelabium similar to *N. maior,* too.

The exuvia differs from all available larvae of *N. maior* by complete absence of mandibular type II-keel, cutting edge distinct, not angulate (Fig. 24H). However, taking into account the notorious variability of Cerambycid mandibles, much larger material is needed to see how reliable the difference really is. Also the pronotum seems to be much more largely microspiculate than in *N. maior,* spines present not only along the lateral furrows but along the pronotal base as well (it is difficult to find out the exact extent of the spines from the damaged exuvia). Supposed maximal length even greater than in *N. maior.*

Host plants: *Fagus, Ulmus, Celtis,* literature gives also *Quercus.* I have found this species in relatively sound wood of dead standing *Celtis australis,* and in inner wood of a hollow in great living *Fagus.*

Distribution: Central and southern Europe, Caucasus, Transcaucasia.

Material: 19. 8. 1976 Bulgaria, Ropotamo, Arkutino, dead adult with cast skin in pupal cell in *Celtis australis,* lgt. et coll. S.

Necydalis morio KRAATZ, 1879

Only two larvae at my disposal. Main stemmata flat, rather indistinct, cuticle behind them ± unpigmented. Third antennal segment stout. Mandibular type II-keel well developed (Fig. 24I). Mala somewhat narrower than in *N. maior,* ligula broader, labial palps slender (see key, Fig. 24E). Prothorax with microscopic spines distributed ± equally on both sides of lateral furrows (as in *N. pennata,* Fig. 24C). Largest available larva 20 mm, CHEREPANOV (1979) gives maximal length 29 mm.

Host plants (CHEREPANOV, l.c.): *Quercus, Acer, Alnus, Fraxinus, Micromeles, Tilia, Padus, Ulmus, Prunus.* Larvae found in sound wood of dead standing stems.

Distribution: Ussuri region, Japan (Hokkaido).

Material: 20. 5. 1976 SU, Khabarovsk, 2/I, *Betula,* lgt. A. V. Kompantsev, coll. IS.

Necydalis pennata LEWIS, 1879 (= *ebenina* BATES, 1884)

One larva and one exuvia available, no hopeful differences found from *N. morio.* Available larva 20 mm; CHEREPANOV (1979) gives maximal length 33 mm.

Host plants (CHEREPANOV, l.c.): *Fraxinus, Alnus, Quercus, Acer, Padus.* Bionomics similar to *N. morio.*

Distribution: Ussuri region, Sakhalin, South Kuriles, Japan.

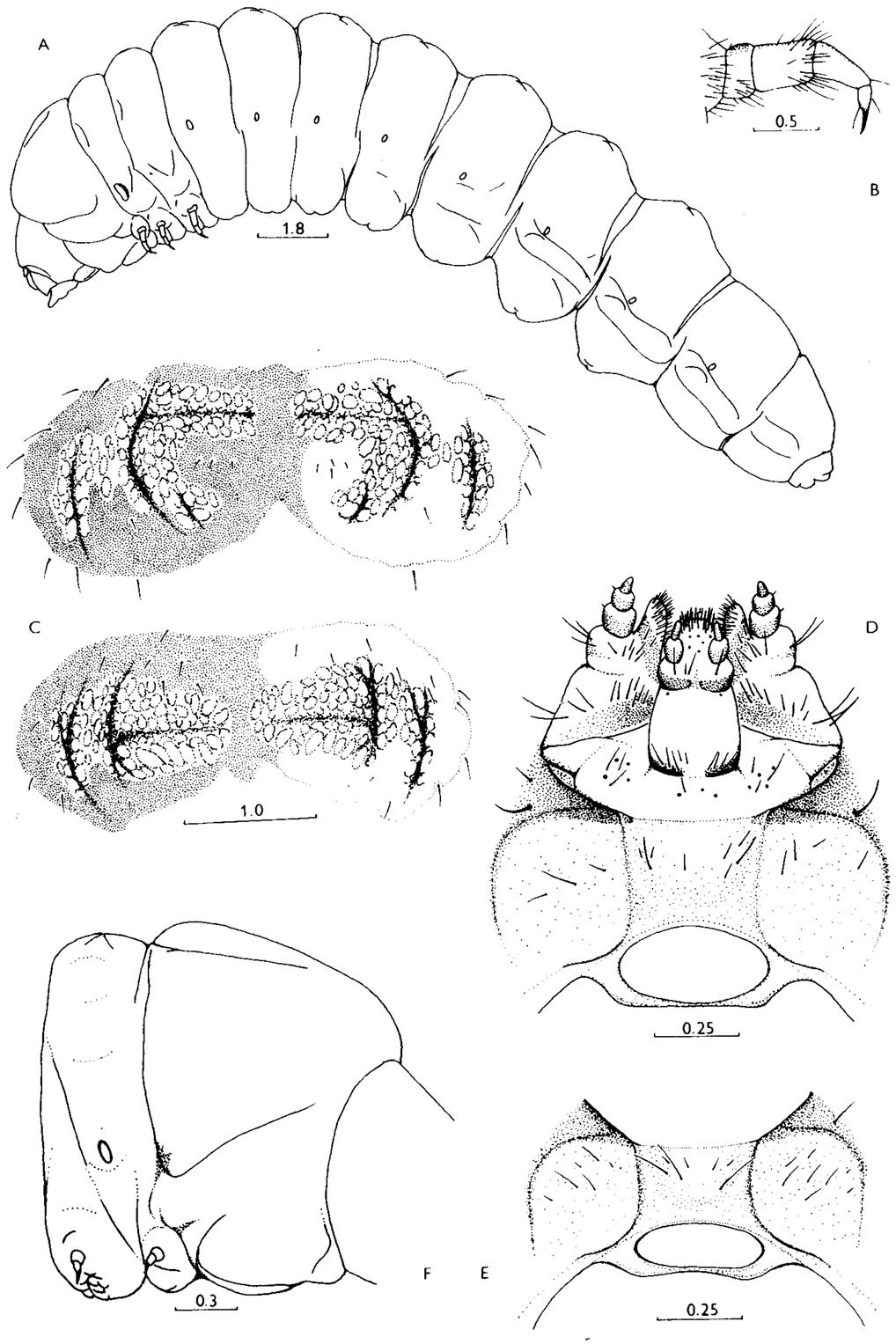
Material: 24. 4. 1969 SU, Ussuri region, Suputinka Nature Reserve, 1/I, *Padus,* B. M. Mamaev lgt., coll. IS; 31. 5. 1985 SU, Sakhalin, Nevel'sk, one exuvia of mature larva, *Betula,* lgt. D, coll. IS.

Subfamily Aseminae THOMSON, 1864

General morphology

Body small to moderately sized, white or yellowish, ± elongate, slightly depressed anteriorly, otherwise cylindrical, broadest at prothorax, slightly broadened posteriorly, with at most moderately long, occasionally rather dense setae.

Head large, usually about by half retracted, in some species largely salient. Cranium occasionally almost as broad as prothorax, ± distinctly transverse, depressed, widest behind middle, sides rounded, rarely almost angulate. Epicranium mostly with rather dense stout often recurved anterior setae (Figs 27H, 28A, 29B, C, 30D, 31C). Both halves fused along whole dorsal length, cranium very shallowly



emarginate or almost cut posteriorly, yet both halves not jointly rounded. Dorsal row of miniature setae present but often incomplete (posterior 1–2 pairs inconstantly present or absent). Adfrontal setae (a seta, or a group of setae, lying originally on epicranium near to postfrontal portion of frontal lines, well developed in most Lepturinae) much reduced or absent, occasionally moved into frontal region *(Nothorhina)*. Frontal lines usually narrow, never strongly S-curved, often rather indistinct in groups with pale unpigmented cranium. Posteriorly frontal lines enter separately the dorsal doubled region, anteriorly they enter or touch the antennal opening, mostly passing to the anterior cranial margin. Transfrontal line absent, or lateral rudiments may be present in some genera (e.g. *Saphanus*). Medial frontal line distinct and complete. 1 + 4 main pairs of frontal setae almost always supplemented by others. Epistomal margin simple, not projecting over clypeus, six or more epistomal setae present, medial and partly also middle pair may be pushed remarkably backwards and rather distant from the frontoclypeal border. Clypeus filling the entire space between dorsal mandibular articulations, ± trapezoidal, at most finely sclerotized at base, often ± distinctly microreticulate, devoid of setae. Labrum of varying shape (cf. Figs 31B and 27A), relatively flat, at least basal sclerotized band present, anterior margin setose, two or more discal setae. Anterior epipharyngeal region with (rarely without) setose areas, tormae of varying shape. Pleurostoma poorly raised, dark, sclerotized, smooth or moderately rugose, subfossal process absent. (As a great exception in the whole family, the pleurostoma of some specimens of certain species may bear some miniature setae.) Gena may be broadly pigmented, at most finely rugose. At most two pairs of main stemmata (no species known with three pairs), dorsal and ventral stemmata may be also developed, but always much less distinct. In Asemini, however, the main stemmata are ± indiscernible in mature larvae, in young larvae often visible, shifted somewhat backwards from their usual position. Hypostomal lines distinct, may or may not reach postoccipital lines. Metatentorial pits very close to hind margin of the ventral sclerite, in some groups in fact absent and the metatentorial arms invaginated from the border between ventral sclerite and the membraneous collar (Atimiini, nearly so in *Vandykea, Anisarthron* - Figs 28B, 25D, E). Metatentorium gracile, metatentorial bridge very thin, metatentorial arms usually only moderately oblique and ± visible on detached head in the ventral view (Figs 25D, E, 27H etc.), only in later instar larvae of the *Asenum*-group more internal and usually almost invisible. Gula moderately to very long, gular lines often raised, medial gular line present (may or may not reach anterior gular margin), or the whole ventral sclerite may be rather pale. Setae present in varying number.

Plate 25: A — *Necydalis maior*, later instar larva, lateral view. (Setae not figured.) B — *N. maior*, mature, left hind leg, anterior view. C — *N. maior*, mature, fourth dorsal (upper) and ventral (lower) ambulatory ampullae. (Microscopic spines not figured on right halves.) D — *Anisarthron barbipes*, mature, labiomaxillary complex, ventral sclerite and metatentorial bridge, ventral view, E — *A. cyrus*, mature, ventral sclerite and metatentorial bridge, ventral view. F — *A. barbipes*. outline of pro- and mesothorax, lateral view.

Antennae well developed, three-segmented (in *Nothorhina* two-segmented), deeply retractile, connecting membrane large. First segment usually long and concealed for the most part in the connecting membrane. Segment 2 rarely longer than broad, segment 3 cylindrical, lateral to lateroventral in regard to the main antennal sensillum, the latter conical, occasionally (e.g. *Atimia*) extremely small. Both mandibular types can be found, with all intermediate situations (Figs 26D, 27I, 30C). Mandibles never too long, border zone usually not striate, outer face often microsculptured, dull. Apical part with two or three ± distinct inner keels present, rarely *(Atimia, Vandykea)* ± absent. Basal part bearing two or more lateral setae, inner face smooth and glabrous. Labiomaxillary complex broadly attached to the anterior cranial margin, cardo free, movable, but in some groups rather small (Fig. 31C). Submentum separated from mentum. Connectig lobe large, flat, undivided. Cardo moderately large to very small, yet the situation of Lamiinae (i.e. cardo completely reduced and the labiomaxillary base firmly attached by whole its width to the anterior cranial margin) never achieved. CRAIGHEAD'S (1923) data about the labiomaxillary complex of *Michthisoma* firmly attached along whole its width, as well as his figure XII/8, are inaccurate, his material of *Michthisoma* at my disposal. Cardo in most groups with a short lateral seta. Stipes usually with broad complete basal sclerotized band. Palpiger large, mala slender, cylindrical, making the impression in ventral view that it grows out exclusively from the palpiger (Figs 26E, 29H). Palpiger process small (Figs 27E, G) or absent. Palps three-segmented, segment 1 without process. Mentum with basal pigmented spots often connected into a transverse continuous band. Praementum usually with basal apodeme unpigmented, i.e. without basal spot. Pigmentation of labial palpigers broadly separate. Ligula and dorsal labial portion with varying pattern of setae and microtrichia (Figs 26J, 30A, B).

Prothorax broadest of body segments, usually slightly depressed. Some prothoracic regions (alar lobes, epipleurum, lateropraesternum) in some groups with remarkably denser setae than other body regions. Lateral furrows distinct, almost reaching anterior prothoracic margin, interrupting anterior pigmented band which is thus divided into four separate patches, the alar lobes may be almost completely sclerotized. The pigmented band occasionally very pale to almost absent. Posterior half of pronotum may be more or less completely covered with microscopic spines (occasionally blunted and becoming minute sclerotized grains, in *Vandykea* they are hair-like microtrichia). Dorsal epipleural border ± complete, but the posterodorsal epipleural angle often much reduced, occasionally almost fused with alar lobe (Fig. 11B), in *Anisarthron* it tends to fuse with mesothoracic epipleurum (Fig. 25F). Alar lobes in some groups with a distinct oblique furrow branching off from the dorsal epipleural border. Epipleurum often sclerotized anteriorly. Ventral epipleural boundary ± obliterated, epipleurum fused with lateropraesternum and at most very poorly separate from the pleural region. Mediopraesternum may or may not be defined. There is a distinct tendency in some groups to develop a transverse fold similar to that of Cerambycinae by fusing of sternellar fold, coxosternum, epimeron and a posterior part of epipleurum (Fig. 11B). Almost all regions may bear microscopic spines, usually less distinct than those on pronotum; best developed in Asemini and partly Atimiini, in Saphanini they are much restricted and indistinct; this is also true for other body microscopic spines. In *Vandykea,* which is apparently close to Atimiini, all the spines (particularly those on ambulatory ampullae) are similar to those on pronotum, i.e. not spine-like, turned into long soft hair-like microtrichia.

Meso- and metanotum divided by X-shaped lines, in some genera almost undivided, in *Vandykea* the posterior arms of the »X« are absent. Postnotum non--developed. In *Atimia* the alar lobes remarkably protuberant. Alar lobes almost or completely fused with the anterior spiracle-bearing epipleural area and the praesternal triangle (Figs 11A, B). Mesothoracic spiracle of varying size and shape, with varying number of moderately large to very small marginal chambers, rarely *(Nothorhina)* no chambers visible in outer view. The spiracle-bearing area not protruding into prothorax. Unlike the abdominal spiracles, the mesothoracic spiracle inclined distinctly backward (Figs 11A, B). Rudimentary metathoracic spiracle always discernible. Pleurum large, undivided, broadly isolating coxa from epipleurum. Coxa poorly defined by short posterolateral and medial impressions, otherwise fused with the surrounding areas. Transsternal line present, occasionally rather indistinct, or incomplete medially. Basisternum divided by at least short oblique converging impressions borne at lateral extremities of the transsternal line.

Distal legs moderately long, four-segmented, but trochanter reduced, tends to fuse with femur. Tibiotarsus and femur may be pigmented. Setae sparse, only femur occasionally with more dense medial subapical setae. Praetarsus uniform, long, slender, elongate conical, acute, without seta, microasperate, its apical portion may be sclerotized.

Ambulatory ampullae on abdominal segments 1 to 7, the seventh ampulla always smaller. Dorsal ampulla with two lateral impressions on each side (Figs 11A, B, 32B), medial impression indistinct in *Vandykea* (Fig. 26A), only one impression on each side in *Pectoctenus* (Fig. 26B). Medial pair of impressions connected by two transverse lines, or only one of them present, or they are absent. Parascutum ± fused with spiracular area. Spiracles similar to the mesothoracic one, smaller (equally large, however, in *Northohina*), spiracles 1 and less distinctly also 8 usually larger than other abdominal spiracles. When elliptical, the abdominal spiracles are inclined forward. Epipleurum of segments 1 to 7 non-protuberant, its anterior portion ± fused with spiracular area, and the whole lateral region of the segment is then divided by a long oblique furrow - the resulting situation rather similar to that of pterothoracic segments (Figs 11A, B). Pleural tubercles present, usually elliptical and poorly defined at their ventral extremity. Pleural discs absent. Epipleurum of segments 7 to 9 protuberant. Pleural tubercles 7 and 8 present, or the eighth, or both *(Tetropium)* lacking. Ventral epipleural border on segments 1 to 7 obscure. Small inconspicuous praesternal triangle fused with epipleurum. Venter often with lateral muscle

marks, but no distinct furrow developed separating the pleural lobe. Ventral ampulla with one longitudinal impression on each side, transsternal line present, may be interrupted or very indistinct. In some genera (mainly in *Saphanus,* Fig. 27C) there is a complex pattern of supplementary lines. Urogomphi present either in all larval instars (the available first instar larvae of Saphanus have large distinct urogomphi which have been observed to be used as one of the egg-bursting devices), or the urogomphi may be lacking in very young larvae (not only in the first instar larvae, but occasionally also in some following instars), this apparently concerns many if not all Asemini. In *Nothorhina* the urogomphi are extremely reduced (Fig. 28C) or absent. Anal segment short, terminal, never fusing with segment 9, never used as a locomotory organ. Anus triradiate, facing caudad and only very slightly ventrad, anal papillae usually small and well separate from segment 10 (Figs 26G, H, 27K, 29D to G etc.) except for *Nothorhina* (Fig. 28C).

Distribution: Aseminae are predominantly Holarctic, with sparse representatives in Oriental and Ethiopian Regions. There are no indigenous species in Australian and Neotropical Regions, except for some species from Central America and the Antilles, which are evidently outsprings of the Holarctic fauna. However, some species have been introduced (*Arhopalus tristis* in New Zealand - HOSKING, 1970; *A. syriacus* in New South Wales, Australia - DUFFY, 1963).

Habits: As far as known, all Aseminae are bound to woody plants, feeding usually in or under bark, or in the wood. Rarely *(Nothorhina)* they attack living healthy trees, but usually they feed on dying, dead or decomposed material, the first two groups occasionally causing some harm. Some species (*Anisarthron, Alocerus, Schurmannia* etc.) feed almost exclusively in wood of dead parts of living trees (died out parts resulting from wounds, bases of dead branches etc.), often sunken behind a living callus. Certain species are ± pronounced root feeders (various groups, but mainly the genus *Spondylis*). The genus *Paratimia* is exceptional by feeding in pine cones. Pupation always in the food material. Adults are often crepuscular or nocturnal, never brightly coloured, usually ferrugineous, brown or black. They are never found on flowers, some species apparently do not feed at all in the adult stage. Certain species are flightless.

Classification: Larvae of the following genera are known and available to me: *Anisarthron, Pectoctenus, Alocerus, Schurmannia, Saphanus, Michthisoma, Oxypleurus, Atimia, Paratimia, Vandykea, Nothorhina, Tetropium, Spondylis, Asemum, Megasemum, Arhopalus* (*Drymochares* has been included under *Saphanus*). The larvae could be provisionally arranged into three tribes:

1) Saphanini *(Anisarthron, Pectoctenus, Alocerus, Schurmannia, Saphanus, Michthisoma, ?Oxypleurus).* Unlike other Saphanini and all Atimiini, the genus *Anisarthron* has numerous stout apical and dorsal setae on ligula - in other Saphanini they are absent or *(Michthisoma)* sparse. *Pectoctenus* differs from all other known Aseminae by the simple lateral impressions on dorsal ampullae (Fig. 26B), but generally the larvae are similar to e.g. *Alocerus* and *Schurmannia. Michthisoma* apparently very similar to *Saphanus,* but only larval skins available of the former, many characters are therefore inaccessible. *Oxypleurus* differs considerably from other Saphanini, both morphologically and ecologically (feeding in *Pinus*, other Saphanini known only from deciduous trees, only in Saphanus there are some data about

feeding in conifers, which, however, require confirmation), and should be perhaps given a tribe of its own, or may be even closer to some of the following two tribes (whose species, on the contrary, are known exclusively from coniferous trees).

2) Atimiini *(Atimia, Paratimia, ?Vandykea).* The genus *Vandykea,* although very distinctive, seems to show certain relations to Atimiini. This relationship is supported by the larva feeding in Cupressaceae like all known *Atimia*-species.

3) The genera *Nothorhina, Tetropium, Spondylis, Asemum, Megasemum* and *Arhopalus* comprise a well-defined tribe Asemini.

Key to all known genera of Aseminae

(non-Palaearctic genera in brackets)

1(18) One or two distinct main stemmata present, ± touching pleurostoma and lateroventral portion of antennal ring (Fig. 26F). Posterior half of pronotum devoid of microscopic spines (Fig. 26C), or if they are present (rather restricted - *Atimia,* Fig. 28A, or very long and hair-like - *Vandykea*), then anterior epipharyngeal region (underside of labrum) and dorsal portion of labium devoid of setae.

2(9) Labrum cordate to subcircular (Fig. 26C), at most slightly shorter than broad.

3(8) Ventral sclerite pale, flat (Figs 25D, E). Mandibular type I (Fig. 26D).

4(5) Ligula bearing numerous very stout apical and dorsal setae (Fig. 25D). Ampullae inconspicuously granulate . . . . . *Anisarthron*

5(4) Ligula without apical and dorsal setae, covered with distinct microtrichia (like in *Saphanus,* Fig. 26J, but narrower, longer, more rounded). Ampullae not granulate.

6(7) Dorsal ampullae with one deep impression on each side (Fig. 26B). Six epistomal setae . . . . . *(Pectoctenus)*

7(6) Dorsal ampullae with two impressions on each side (cf. Fig. 11A). More than six epistomal setae . . . . . *Alocerus, Schurmannia*

8(3) Ventral sclerite ± abruptly transversely raised, roof-like, pigmented (Fig. 27H). Mandible with narrow striate type II-keel present (Fig. 27I) . . . . . *Oxypleurus*

9(2) Labrum transverse, at least twice shorter than broad (Figs 27A, 28A).

10(13) Anterior epicranial setae very sparse (Fig. 27A).

11(12) Ligula without apical and dorsal setae (Fig. 26J) . . . . . *Saphanus*

12(11) Ligula with sparse apical and dorsal setae. (Note: Both antennae and maxillary palps are three-segmented, not two-segmented as stated by CRAIGHEAD, 1923, p. 103; also the labiomaxillary complex is not attached to cranium for its entire width, cardo free, movable, although small) . . . . . *(Michthisoma)*

13(10) Anterior epicranial setae dense, stout (Fig. 28A).

14(15) Ampullae of segments 4 to 6 remarkably different from others, deeply bilobed, each lobe strongly protuberant (Fig. 27J). Ventral sclerite ± raised (Fig. 28B) . . . . *Atimia*

15(14) Ampullae uniform, not or only moderately bilobed. Ventral sclerite flat.

16(17) Body almost devoid of microscopic spines or microtrichia (but see note under *Paratimia* following this key). Setae moderately dense, finer, pale . . . . . *(Paratimia)*

17(16) Hind half of pronotum, ambulatory ampullae and certain other areas covered with very long dense ferrugineous hair-like (not spine-like) microtrichia, body setae extremely dense, very short, stout, bright ferrugineous (Fig. 26A) . . . . . *(Vandykea)*

18(1) Main stemmata in later instar larvae indiscernible, in younger larvae usually visible, then moved remarkably backwards, not touching pleurostoma. Posterior half of pronotum

always distinctly ± entirely microspiculate (Figs 28H, 30D, 32A). Anterior epipharyngeal region and dorsal portion of labium with dense stout setae (Figs 28D, E, 29A, 30A, B).

19(20) Antennae large, two-segmented (Figs 28G, H). Tormae T-shaped, with long distinct anterior branch (Fig. 28E). All functional spiracles of about same size, without externally visible marginal chambers (Fig. 28F). Anal papillae very large, fused with anal segment (Fig. 28C) . . . . . *Nothorhina*

20(19) Antennae much shorter, three-segmented (Figs 29B, C, 30D, E, F). Tormae not T-shaped (Fig. 29A). Mesothoracic spiracle much larger than abdominal ones, all spiracles with two to many ± distinct (occasionally very small) marginal chambers (Fig. 28I). Anal papillae smaller, ± separate from anal segment (Figs 29D to G, 32C to J).

21(22) Mandibular type I. Ventral sclerite very short in middle (width/medial length ratio over 4). Labrum strongly transverse (Figs 29B, C) . . . . . *Tetropium*

22(21) Mandibular type II, with large keel and distinct striated plates (Fig. 30C, the type II-keel may be very much reduced in extremely young larvae). Ventral sclerite longer (in mature larvae below 3 - Fig. 31C, never over 4). Labrum long, only in some very young larvae distinctly transverse (Figs 31A, B) . . . . . *Asemum*-group

The following material of the four non-Palaearctic genera available (the genera are monotypic except for *Pectoctenus*):

Pectoctenus FAIRMAIRE, 1896: *P. scalabrii* FAIRMAIRE, 1896. December 1950 Kenya, Nairobi, three larvae »ex dead part of living *Psidium guajava*«, J. C. M. Gardner lgt., coll. British Museum (No. 1955-563, Com. Inst. Ent. No. 13484).

Michthisoma LECONTE, 1850: *M. heterodoxum* LECONTE, 1850. 1913 USA, North Carolina, Cedar Mountain, one complete and one incomplete exuviae, larvae collected in dead sapwood of stumps of *Hicoria,* F. C. Craighead lgt., coll. U. S. National Museum, Washington (Hopk. US. 9784x).

Paratimia FISHER, 1915: *P. conicola* FISHER, 1915. 2. 10. 1914 USA, Oregon, near Monumental Mines SW of Waldo, one larva from *Pinus attenuata* (cone), J. M. Miller et P. D. Sergent lgt., coll. U. S. Natn. Mus. Washington (Hopk. US. 10856d). (Note: The single available larva apparently mature; one of those described by CRAIGHEAD, 1923, who had at least two larvae at his disposal - p. 35: »Described from specimens . . .«. If they were all mature, then some non-mature larvae should be examined to make sure that the microasperities are really absent in all instars - cf. the introduction to the genus *Atimia,* p. 146).

Vandykea LINSLEY, 1932: *V. tuberculata* LINSLEY, 1932. 19. 6. 1941 USA, California, Mt. St. Helena, one larva from *Cupressus goveniana* (»Sargent cypress«), D. J. et J. N. Knull lgt., coll. Ohio State University, Columbus, Ohio.

Genus *Anisarthron* DEJEAN, 1835

Type species: *Cerambyx barbipes* SCHRANK, 1781 (monobasic)

Body robust, white, with relatively numerous moderately long very thin almost unpigmented setae.

Head rather deeply retracted. Cranium moderately transverse (1.2–1.3), depressed (1.9–2.0), not microreticulate, ± unpigmented except for mouthframe and hypostomal and medial frontal lines. Epicranium with sides moderately roundly convex, bearing numerous anterior setae some of which are rather stout, ± recurved. Usually only anterior two pairs of setae of dorsal rows present. Frontal lines

indiscernible except for anterior extremities touching antennal openings from below and reaching (almost not weakened) anterior cranial margin. Frons almost flat, at most finely rugose. Four pairs of main anterior frontal setae supplemented by other smaller setae which are most numerous in anterior frontal angles above antennae. Epistomal margin narrowly pigmented, abruptly steeply declivous. Usually more than six epistomal setae, relatively close to clypeal border. Clypeus narrow, gently tapering, basal half yellowish, anterior half microreticulate. Labrum slightly transverse, from half-circular to broadly oval. Basal half pigmented, numerous anterior and sparse lateral marginal setae, two strong and a few shorter discal setae. Epipharynx with tormae short, very broad, acutely tapering posteriorly. Two rows of stout setae reaching almost to posterior extremities of tormae, medial group of a few sensilla with a transverse row of four miniature setae. Gena finely pigmented, pigmentation at most about as broad as pleurostoma. Two large convex contiguous (sometimes partly fusing) main stemmata on each side, with large pigment spots (rarely dorsal spot broken in two), pigment of two dorsal and one ventral stemmata often slightly visible, too. Hypostomal lines strongly curved, not reaching postoccipital line. Ventral sclerite unpigmented, slightly convex, moderately long (about 3.5–5.0), anterior margin pigmented in hypostomal region, hind margin ± unpigmented. Gula very broad, with distinctly raised gular lines. Metatentorial pits indistinct, extremely close to hind margin, metatentorial arms only very slightly inclined inwards, metatentorium completely visible in ventral view (Figs 25D, E). Both gular and hypostomal regions bearing some setae.

Antennae rather long, deeply retractile, three-segmented. Segment 2 about as long as broad, segment 3 cylindrical, at least slightly longer than very large elongate main antennal sensillum. Mandibular type I, mandible short, robust, border zone inconspicuous, entire outer face roughly microsculptured. Apical portion with three long inner keels and one shorter ridge leading from dorsal angle distad. Cutting edge simple, with rather inconstantly developed low costa along it on dorsal surface. Basal portion bearing a few lateral setae. Cardo large (for this subfamily), without lateral seta. Stipes with lateral extremity of basal pigmented band pale, indistinct, so are also ventral pigmented areas of palpiger and mala. Palpiger process small, occasionally absent. Third palpal segment elongate, about as long as second. Mentum very distinctly microreticulate, with two basal transverse spots approaching each other, in some specimens connected. Pigmented areas of labial palpigers narrowly separate, or may be ± connected by medial subcuticular spot. Second segment of labial palps very long, cylindrical, about as long as segment 1. Ligula narrow (palps separated by slightly more than their width), covered with extremely stout strong ferrugineous setae.

Body microscopic spines extremely restricted, indistinct, unpigmented.

Prothoracic pigmented band very pale yellow. Posterodorsal epipleural angle much reduced and fused with mesothorax (Fig. 25F). Episternum separated from lateropraesternum. Mediopraesternum sharply defined, bearing up to about

20 setae. Coxosternum separated from sternellar fold, with at most pale inconspicuous pigmented spots.

Meso- and metanotum divided by rather obscure X-shaped lines, metanotum with a few inconspicuous granules about middle. Mesothoracic spiracle very small (much shorter than maxillary palp), with blunt rounded extremities, several marginal chambers at upper extremity. Transsternal lines distinct, lines dividing basisternum present but obsolete on metasternum. Sterna granulate along transsternal lines, granules flat, rather inconspicous, particularly those on mesosternum.

Legs relatively well developed, stout, unpigmented.

Ambulatory ampullae uniform, slightly medially impressed, not bilobed, indistinctly granulate. Dorsal ampullae with two transverse lines ± present. Spiracles very small, distinctly smaller than mesothoracic spiracle, those of segments 1 and 8 larger than others. Hind margin with up to about 6 marginal chambers. Pleural tubercles bearing up to about 10 setae each, tubercles of segments 7 and 8 ± distinct. Ventral ampullae with transsternal line present. Sharp long slender urogomphi pointed obliquely upwards, rather broadly distant. Anal papillae very small, sharply separate from anal tube, bearing some short setae.

Apparently two species known:

1(2)! Gula slightly longer (Fig. 25D). Central Europe . . . . . *barbipes*
2(1)! Gula slightly shorter (Fig. 25E). Talysh, North Iran . . . . . *cyrus*

Anisarthron barbipes (SCHRANK, 1781)

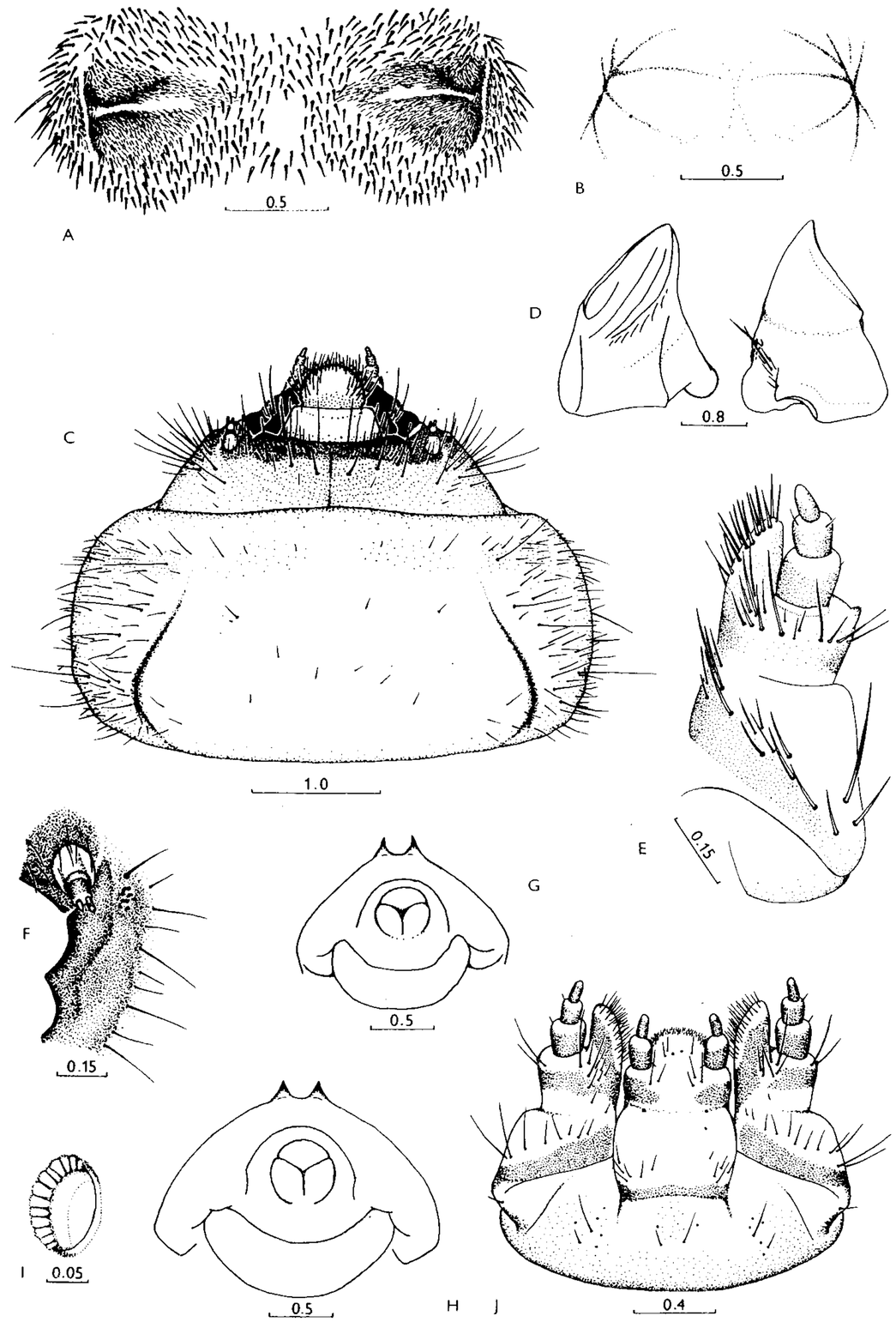
Head pigmentation darker, in mature larvae mouthframe very dark brown. Gula in later instar larvae slightly longer, its anterior margin ± straight (Fig. 25D). All spiracles in later instar larvae with several marginal chambers. Length up to 16 mm.

Bionomics: Polyphagous on deciduous trees. Larvae always in dead parts of living trees, in dead wood in contact with living tissue (hollows, dead parts after wounds, or at bases of died out branches surrounded by living callus). The wood of rather dark brownish colour. At least two- or three-year life-cycle. Occasionally found together with *Pedostrangalia revestita* or *Rhamnusium bicolor* (Lepturinae). Pupation in wood in spring, flight period June to July.

Distribution: Central Europe, up to northern Italy and North of the Balcan Penninsula.

Material: CS, various spots, 1976–83, about 70 larvae from *Fagus, Ulmus, Populus, Alnus, Juglans,* lgt. et coll. S.

Plate 26: A — *Vandykea tuberculata,* later instar, third dorsal ambulatory ampulla. B — *Pectoctenus scalabrii,* later instar, dividing of third dorsal ambulatory ampulla. C — *Schurmannia sicula,* later instar, head and prothorax, dorsal view. D — *S. sicula,* later instar, left mandible, dorsal (right) and medial (left) views. E — *S. sicula,* later instar, left maxilla, lateroventral view. F — *S. sicula,* later instar, left pleurostoma, gena and antenna, anterior view. G — *S. sicula,* later instar, outline of abdominal segments 9 and 10 in posteroventral view, showing urogomphi. H — *Alocerus moesiacus,* later instar, dtto. I — *A. moesiacus,* later instar, right spiracle of abdominal segment 1. J — *Saphanus piceus,* mature, labiomaxillary complex, ventral view.



Anisarthron cyrus (VILLIERS, 1971)

Extremely similar to *A. barbipes,* best distinguished by its distribution. Head pigmentation paler, mouthframe even in mature larvae bright ferrugineous. Gula slightly shorter, its anterior margin gently emarginate. Marginal chambers less distinct, even in mature larvae often only two chambers present, if more, then others usually very indistinct. Available larvae slightly smaller than largest available larvae of *A. barbipes*. The largest larva is contracted so that it is difficult to estimate the natural length.

Larvae have been found in *Carpinus*. Habits similar to *A. barbipes*.
Distribution: Talysh (S-E corner of the Soviet Transcaucasia), North Iran.
Material: 13. 4. 1979 SU, Talysh, Avrora, 4/I, *Carpinus,* lgt. D, coll. IS.

Genus Alocerus MULSANT, 1862

Type species: *Alocerus fulvus* MULSANT, 1862 = *Callidium moesiacum* FRIVALDSZKY, 1838 (monobasic)

Genus *Schurmannia* SAMA, 1979

Type species: *Schurmannia sicula* SAMA, 1979 (monobasic)

The larvae of the two genera appeared very similar and are best treated together.

Body white, moderately elongate, with moderately long numerous relatively fine setae.

Head deeply retracted, much narrower than prothorax (Fig. 26C). Cranium moderately transverse (1.34), depressed (2.04, one specimen of *Schurmannia* measured), not microgranulate, almost unpigmented excepting mouthframe. Sides of epicranium very feebly convex, anterior setae not very numerous, not distinctly recurved, dorsal rows present but usually incomplete. Frontal lines obscure due to unpigmented cranium; anteriorly frontal lines passing through antennal openings and distinctly reaching anterior cranial margin. Frons ± flat. Four main anterior frontal setae supplemented by varying number of others. Epistomal margin narrowly pigmented, abruptly steeply sloping. In all available larvae more than 6 epistomal setae present (about 10 to 14), moderately distant from clypeal border except for lateral pair. Clypeus moderately broad, gently tapering. Labrum long, roundly cordate, nearly as long as wide, with broad strongly sclerotized basal band, central area yellowish, broad anterolateral margin unpigmented, bearing moderately numerous long setae, two main discal setae accompanied by a few thinner ones. Tormae short, oblique, broad, slightly curved, without anteromedial branch. Anterior epipharyngeal area with numerous setae. Pleurostoma often bears a few

minute setae! Pigmentation of gena narrower than width of pleurostoma, reaching at most very narrowly behind main stemmata, most of anterior epicranial setae lie in unpigmented region. Main stemmata very distinct, two on each side (Fig. 26F) or fusing into one. Other stemmata without pigment, hardly discernible. Hypostomal lines finely pigmented, by far not reaching postoccipital line. Ventral sclerite smooth, ± flat, completely pale, short (about 5.0), hind margin unpigmented, deeply roundly emarginate (not angulate). Anterior margin of hypostomal region pigmented, gula very broad, gular lines slightly raised, anterior margin unpigmented. Metatentorial pits short, close to hind margin, metatentorial arms only moderately oblique, completely visible in ventral view. Gula bearing a few setae.

Antennae rather long, three-segmented, deeply retractile. First segment very long. Third segment elongate, distinctly longer than large robust main sensillum. Mandibular type I (Fig. 26D), mandible short, robust, apex prominent, dorsal angle blunt. Border zone indistinct, whole outer face very roughly microsculptured. Apical portion with three inner keels, cutting edge simple, dorsal face with low indistinct ridge along cutting edge. Basal portion with two longer and some shorter lateral setae. Submentum with two, connecting lobes with greater number of setae. Cardo large, in available specimens without seta. Basal band of stipes laterally pale, palpiger with pigmentation restricted to lateral face, and with short blunt laterodorsal process. Mala with ventral pigmentation obsolete. Third segment of maxillary palp elongate, about as long as second (Fig. 26E). Mentum with basal pigmentation continuous or narrowly interrupted; may or may not be microreticulate. Pigment of labial palpigers separate. Second segment of labial palps elongate. Ligula narrow (palps separated by about 1.5 of their width), without basal spots, two ventral setae, apical and inner margin covered with dense distinct reddish microtrichia.

Body devoid of microscopic spines, or they are extremely inconspicuous (except for those along anterior prothoracic margin).

Prothoracic band extremely indistinct, pale yellowish. Epipleurum ± unpigmented, posterodorsal angle much reduced. Mediopraesternum defined, bearing about 10 setae. Episternum separated from lateropraesternum. Coxosternum separate, coxal portion without pigmented spot.

Meso- and metanotum divided by X-shaped lines. Mesothoracic spiracle small (much shorter than maxillary palp), with numerous distinct marginal chambers. Transsternal lines and lines dividing basisternum distinct, sterna non-granulate.

Legs relatively long and slender, unpigmented.

Ampullae non-granulate, dorsal ampullae with two indistinct transverse lines present; very shallowly impressed medially. Spiracles small, broadly oval, with up to about 15 distinct marginal chambers along hind margin (Fig. 26I). Spiracles 1 and 8 larger than others, first spiracle much smaller than mesothoracic one. Pleural tubercles bearing 2 (−3) long and some short setae, tubercles 7 and 8 present. Ventral ampullae very shallowly impressed medially, transsternal line present. Urogomphi

large, separated by more than their basal width (Figs 26G, H). Anal papillae small, sharply separate from anal tube, bearing numerous short setae.

The genus *Schurmannia* is monotypic, and the Palaearctic forms described in *Alocerus* are considered ± conspecific, too.

1(2)! Main stemmata almost without dark pigment spots. Central area of mentum almost not microreticulate. Urogomphi shorter, inner sides diverging (Fig. 26H). Mediterranean area, but not known from Sicily . . . . . *Alocerus moesiacus*

2(1)! Main stemmata better developed, with large dark pigment spots (Fig. 26F). Central area of mentum distinctly microreticulate. Urogomphi longer, inner sides ± parallel (Fig. 26G). Sicily . . . . . *Schurmannia sicula*

Alocerus moesiacus (FRIVALDSZKY, 1838)

One single larva available. Main differences in the key. The available larva with one main stemma on each side, less distinct. Antennae shorter, segment 2 slightly transverse. Cranium very smooth, shining. Spiracles with relatively slightly larger marginal chambers (Fig. 26I). Head and body setae distinctly pigmented, ferrugineous. Length 14 mm.

Bionomics: Larvae feed in various deciduous trees (*Ficus, Ulmus, Platanus* etc.). M. Sláma (personal communication) has reared this species from dead barkless part of living *Platanus*, from moist dark rotting wood - apparently the habits are similar to *Schurmannia, Anisarthron* etc.

Distribution: Mediterranean area (Iberian Penninsula, Italy?, Greece, Turkey, Syria).

Material: Greece, Larisa, one larva from *Ulmus* sp., P. Schurmann lgt., G. Sama coll.

Schurmannia sicula SAMA, 1979

Main differences in the key. Main stemmata more often two on each side, very distinct (Fig. 26F). Antennae longer, segment 2 in later instar larvae at least as long as broad. Certain cranial areas (e.g. gena at bases of hypostomal lines) relatively distinctly microreticulate, dull. Spiracles mostly with marginal chambers slightly smaller. Head and body setae almost unpigmented, yellowish. Largest available larva 16 mm.

Bionomics (SAMA, 1979, SAMA et SCHURMANN, 1980): *Acer* is the only known host. Larvae live in dead wood of living trees in contact with living tissue, apparently similarly to *Anisarthron*. Development period at least 2–3 years. Pupation in spring (pupae found May 30th).

Material: 1979 Italy, Sicily, Piano Zucchi, 3/I, *Acer* sp., G. Sama lgt., coll. S.

Genus *Saphanus* SERVILLE, 1834 (incl. *Drymochares* MULSANT, 1847)

Type species: *Callidium piceum* LAICHARTING, 1784 (monobasic)

Body white, with sparse relatively short ferrugineous setae.

Head rather deeply retracted, distinctly narrower than prothorax. Cranium moderately transverse (about 1.3), depressed (about 2.1–2.3), only very feebly microreticulate. Epicranium with sides moderately roundly convex (Fig. 27A), anterior setae very few, not distinctly recurved, dorsal rows present, incomplete. Frontal lines discernible along whole length, narrow, enter antennal openings, leave them much weakened and reach anterior cranial margin. Frons flat, posterior half almost unpigmented, anteriorly gradually darker, epistomal margin broadly intensively pigmented. Distinct lateral rudiments of transfrontal line may be present. Four pairs of main anterior frontal setae, other setae at most very few and miniature. Epistomal margin abruptly obliquely declivous, six strong epistomal setae, middle and esp. medial pair distinctly removed back from clypeal border. Clypeus broad, strongly tapering. Labrum very short, transversely oval, basal half pigmented, anterior margin with sparse strong setae, two ± isolated discal setae. Epipharynx anteriorly with two areas of sparse setae (Figs 27D, F), tormae broad and transverse at base, then curved abruptly backwards, parallel, tapering. Between them a very distinct transverse row of setae and other sensilla. Gena broadly pigmented (about 2–3 times as broad as pleurostoma), pigmentation gradually disappears posteriorly. Two pairs of large convex main stemmata with distinct pigment spots. Dorsal stemmata (two or fusing) and ventral stemma usually also with discernible pigment spots, although their cuticular components obsolete. Hypostomal lines ± reaching postoccipital line. Ventral sclerite short (about 4.0–5.0), gently convex, finely pigmented (slightly paler than gena). Metatentorial pits long, narrow, very close to hind margin, latter somewhat darkened. Gula very broad, at most slightly raised, bearing 1–2 pairs of setae, broad medial pale area in full width reaching anterior margin. Hypostomal region glabrous. Metatentorium well visible in ventral view.

Antennae moderately long, three-segmented. Second segment at most as long as broad, main sensillum large, longer than broad, third segment elongate, as long as, or slightly longer than main sensillum. Mandibular type I, apex and dorsal angle prominent, not very sharp, cutting edge simple, shallowly emarginate. Three distinct long inner keels (their joined posterior extremities project in dorsal view behind dorsal angle as a ± distinct supplementary tooth), one short inner ridge at dorsal angle. Outer face entirely very distinctly microsculptured, border zone impressed, somewhat step-like, not striate. Basal portion with two long and several shorter setae on lateral face. Labiomaxillary complex (Fig. 26J) with relatively sparse stout setae. Cardo moderately large, usually bearing small lateral seta. Stipes, mala and palpiger with ventral pigmentation complete and distinct. Palpiger process present (Figs 27E, G). Third segment of maxillary palps elongate, about as long as second. Mentum almost not microreticulate, basal band ± continuous, narrower medially. Pigmentation of labial palpigers separate. Ligula broad (palps separated by almost twice their width), short, with two (or at most 3–4) ventral setae, apical

and inner margins covered with short microtrichia, broad medial dorsal area smooth. Second segment of labial palps elongate.

Prothoracic band bright yellow-orange, epipleurum with distinct anterior pigmented spot, posterodorsal epipleural angle well defined (Fig. 11A). Mediopraesternum well defined, bearing about 6(−8) setae. Episternum separated from lateropraesternum. Coxosternum sharply separated from sternellar fold, anterior region of sternellar fold and medial regions of both halves of coxosternum finely microspiculate. Coxal region of coxosternum without pigmented spot.

Meso- and metanotum divided by distinct X-shaped lines, mostly with fine microscopic spines (may be extremely indistinct or absent in mature larvae). Mesothoracic spiracle small, in later instar larvae distinctly shorter than maxillary palp, up to 8−10 small marginal chambers at upper extremity. Sterna non-granulate, transsternal lines distinct, lines dividing basisternum less so, mesobasisternum occasionally with small microspiculate areas at these latter lines.

Legs moderately long, rather stout, femur and tibiotarsus brightly pigmented laterally.

Ampullae non-granulate, usually with small areas of fine microscopic spines, particularly at hind margin. Dorsal ampullae shallowly impressed medially, two transverse lines ± present. Spiracles small, broadly oval, posterodorsal margin with up to about 12 distinct marginal chambers; spiracles much smaller than mesothoracic one, spiracle 1 and also 8 slightly larger than others. Pleural tubercles with 2(−3) setae, tubercles 7 and 8 present. Ventral ampullae shallowly impressed medially, showing very complex pattern of numerous supplementary lines so that esp. on posterior ampullae there are several ± complete transverse lines (Fig. 27C). Slender long sharp broadly separate sclerotized urogomphi (Fig. 27B) pointed obliquely upwards. Anal papillae moderately large, relatively distinctly separate from anal segment, bearing a few short setae.

Four or five species known, larvae of two of them at my disposal. Unexpectedly, although at present usually classified in two separate genera, they are extremely similar to each other and no really reliable differences have been found. As far as the larval morphology concerns, *Drymochares* cannot be accepted as a separate genus.

Saphanus (s. str.) *piceus* (LAICHARTING, 1784)

All pigmentation (head, prothorax) from bright yellow-orange to orange-ferrugineous. Process of maxillary palpiger usually short (Fig. 27E), often only low blunt tubercle. Anterior epipharyngeal setae ± reaching bases of tormae (Fig. 27D). Length up to 30 mm.

Bionomics: Polyphagous, but deciduous trees decidedly preferred, I have never found larvae in conifers. Larvae feed in dead standing trees or in stumps of various diameter, always at the ground level or usually underground, in wet rotting wood. Pupation at the top of a longer

vertical gallery, emergence mostly above ground level. Pupation in spring and early summer, beetles in summer. They are nocturnal, crawl on the ground, often found in pitfall traps. During the day they are usually hidden under logs, loosen bark etc. At least three-year life-cycle.

Distribution: Central and northern S. Europe - the Alps and adjacent regions. Not found in Transcaucasia as often misquoted in literature.

Material: 1977 - 84 CS, Bohemia, various spots, about 50 larvae from *Fagus, Quercus, Carpinus, Betula, Salix, Prunus,* lgt. et coll. S.

Saphanus (*Drymochares*) *starcki* (GANGLBAUER, 1888)

Extremely similar to *S. piceus,* distribution is the best distinguishing character. All head pigmentation more »dull«, usually yellow to brown, without bright orange component, or it is less distinct than in *S. piceus*. Maxillary palpiger process usually longer (Fig. 27G). Anterior epipharyngeal setose areas not reaching to tormae, or at most by single setae (Fig. 27E). Largest avail. larva 23 mm.

Bionomics apparently similar to *S. piceus*. Known only from deciduous trees (data in literature about *S. piceus* feeding in conifers should be, in my opinion, provided with question mark until confirmed).

Distribution: Eastern Black Sea region (West Caucasus to Turkey).

Material: 1957 - 81 SU, Krasnodar region, various spots, 17/I (some series), *Fagus, Betula, Buxus,* B. M. Mamaev, A. I. Miroshnikov and D. lgt., coll. IS.

Genus *Oxypleurus* MULSANT, 1839

Type species: *Oxypleurus nodieri* MULSANT, 1839 (monobasic)

Body white, moderately elongate, with relatively long stout rusty brown setae.

Head only moderately retracted, distinctly narrower than prothorax. Cranium moderately transverse (about 1.4), distinctly depressed (about 2.0 due to strongly raised ventral sclerite), only underside anteriorly ± microreticulate. Epicranium rather pale, sides distinctly roundly convex, anterior setae rather numerous, strong, recurved (Fig. 27H), dorsal rows usually incomplete. Frontal lines distinct, slightly curved, through antennal openings reaching anterior cranial margin. Frons remarkably longitudinally convex, gently sloping towards clypeus including epistomal margin (in other Aseminae frons usually ± flat and epistomal margin ± abruptly declivous). Frons in later instars ± pigmented, anterior half darker. Four strong anterior setae with some smaller ones esp. in anterior frontal angles. Epistomal margin gently obliquely sloping, very dark, narrow. Six epistomal setae, middle and esp. medial pair separate from clypeal border. Clypeus narrow, feebly microreticulate. Labrum cordate, slightly shorter than broad, overall pigmented except at apex. Sparse marginal setae, one pair of strong separate discal setae. Epipharynx with numerous anterior setae, tormae short, broad, oblique, not angulate, without anteromedial branch. Gena broadly pigmented, becoming gradually paler posteriorly (Fig. 27H). One main stemma, often abruptly prominent, facing forward, with

one or sometimes two distinct pigment spots. Dorsal stemmata almost indiscernible, ventral stemma absent. Hypostomal lines disappearing just before postoccipital lines. Ventral sclerite moderately long (about 3.0), intensively pigmented, abruptly transversely raised, roof-shaped (Fig. 27H). Gula feebly raised, medial gular line posteriorly narrow, anteriorly broadened into large triangular spot, reaching anterior margin. About five pairs of gular setae, hypostomal region almost glabrous. Metatentorial pits short, indistinct, very close to hind margin, latter shallowly emarginate. Metatentorium visible in ventral view.

Antennae moderately long, three-segmented. Third segment cylindrical, much longer than large elongate main sensillum. Mandibular type II, apex prominent, dorsal angle short border zone finely striate. Apical portion with three inner keels, inner striated plate reduced, dorsal plate present, with only a few (about three) ridges, laterally delimited by sharp carina connecting apex and dorsal angle (Fig.27I). Outer face of apical portion smooth, ± shining. Basal part with lateral face very roughly microsculptured (sharply contrasting with smooth spical part), bearing two strong setae (according to DUFFY, 1957, who had at hand South African larvae, there are up to four lateral setae). Submentum bearing about 2–4 setae. Cardo large, usually with lateral seta. Stipes, palpiger and mala with distinct ventral pigmentation, distinct short palpiger process present. Segment 3 of maxillary palp elongate, about as long as segment 2. Mentum feebly microreticulate, with continuous basal band. Ligula narrow (palps separated by about 1.5 of their own width), having two large basal pigmented spots, usually with two ventral setae, apical and dorsal margins covered with very dense short reddish microtrichia. Pigmented areas of labial palpigers separate, second palpal segment slender, elongate.

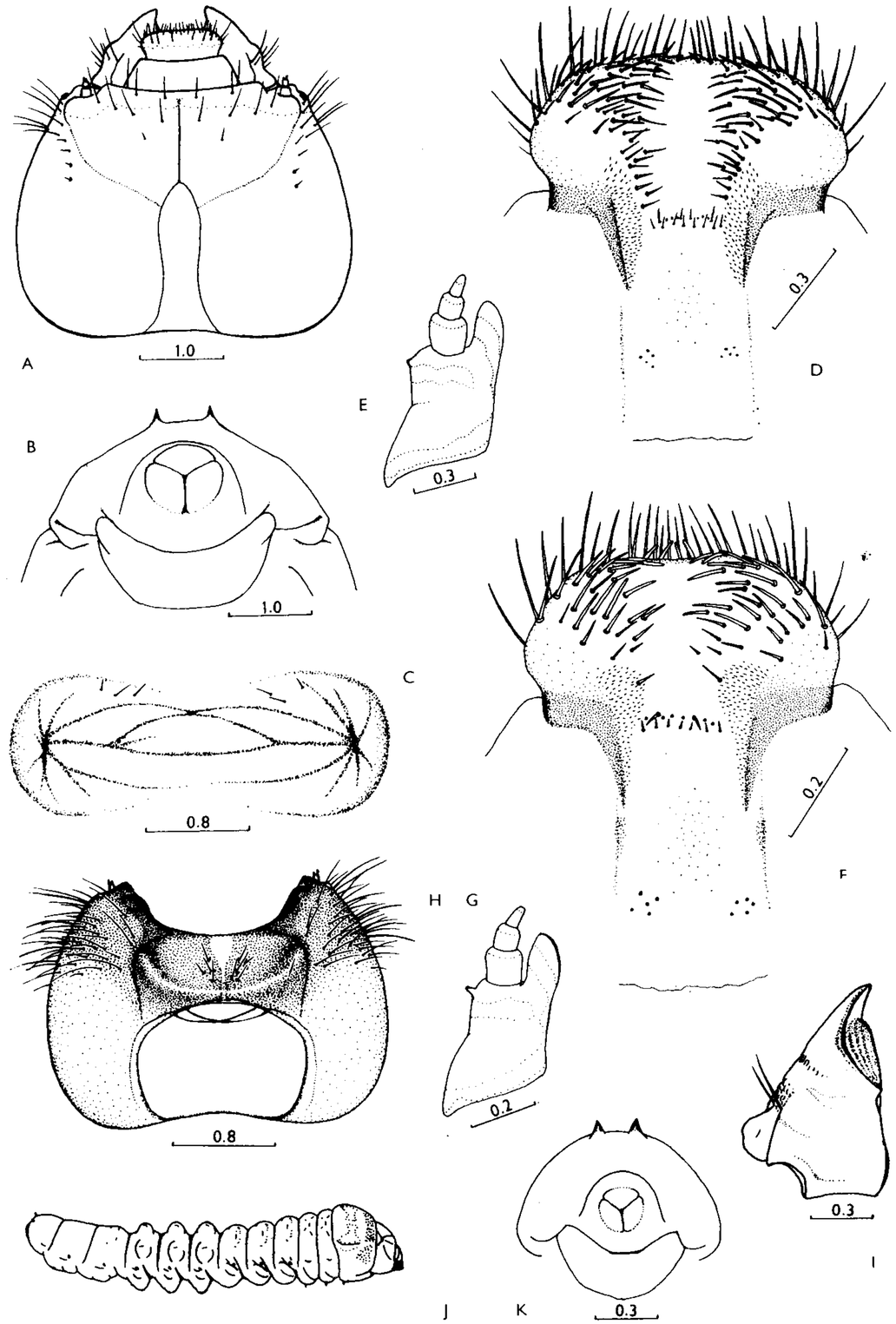
Body essentially devoid of microscopic spines, or they are extremely inconspicuous.

Prothoracic band narrow, pale, yellow, epipleurum anteriorly yellowish. Posterodorsal epipleural angle reduced, not fused with alar lobe or mesothoracic epipleural region. Mediopraesternum rather distinctly defined, with up to about 10 setae. Coxosternum separate from sternellar fold, coxal portion without pigmented spot. Episternum separated from lateropraesternum.

Meso- and metanotum divided by distinct X-shaped lines. Mesothoracic spiracle small, with about 2–4 moderately large marginal chambers at upper extremity. Transsternal lines and lines dividing basisternum relatively distinct, sterna along transsternal lines granulate.

Legs slender, rather long, femur and tibiotarsus at most pale yellowish.

Plate 27: A — *Saphanus piceus,* mature, head, dorsal view. B — *S. piceus,* later instar, outline of abdominal segments 9 and 10 in posteroventral view, showing urogomphi. C — *S. piceus,* mature, third ventral ambulatory ampulla. D — *S. piceus,* mature, epipharynx. E — *S. piceus,* mature, outline of distal right maxilla, lateroventral view. F — *S. starcki,* later instar, epipharynx. G — *S. starcki,* later instar, outline of distal right maxilla, lateroventral view. H — *Oxypleurus nodieri,* later instar, cranium, ventral view. I — *O. nodieri,* later instar, left mandible, dorsal view. J — *Atimia,* later instar larva, laterodorsal view. (Setae not figured. Drawn according to the photograph of *A. dorsalis* in CRAIGHEAD, 1923, pl. XXV, fig. 4. No scale.) K — *A. nadezhdae,* half-grown, outline of abdominal segments 9 and 10 in posteroventral view, showing urogomphi.



Ampullae granulate. Dorsal ampullae deeply narrowly medially impressed, two incomplete transverse lines present. Spiracles much smaller than mesothoracic one, broadly oval, hind margin with 2–4 distinct marginal chambers. Spiracles 1 and 8 larger than others. Pleural tubercles with 2 long and sometimes 1–2 short setae, tubercles 7 and 8 present. Ventral ampullae deeply medially impressed, transsternal lines indistinct, interrupted. Urogomphi sharp, long, often incurved, both spines separated by much more than their basal width. Anal papillae small, sharply separate from anal segment, bearing very few setae.

Two species known, one at my disposal.

Oxypleurus nodieri MULSANT, 1839

Largest available larva 18 mm.

Host plant: *Pinus*. Little is known about bionomics. The larva feeds in dead wood, sometimes found in structural timber. Two- or more-year development (DUFFY, 1957, based on data concerning habits of the South African population). M. Sláma (personal communication) found larvae in wood of dead barkless region on living *Pinus*, so the habits are apparently similar to those of *Anisarthron* or some other Saphanini.

Distribution: Mediterranean area (incl. Canary Islands), as far eastwards as the Black Sea. In addition, the species is known from South Africa (see DUFFY, 1957), but actual status of that population is not clear.

Material: Canary Islands, Teneriffa, Las Mercedes, one larva from *Pinus*, P. Schurmann lgt., M. Sláma coll; 1. 6. 1975 Spain, Ports de Beseit, Tarragona, 1/–, host not stated, E. Vives lgt. et coll; June 1984 Greece, Trypi, 1/I, *Pinus*, M. Sláma lgt. et coll; 30. 3. 1976 SU, Crimea, 3/?, *Pinus*, lgt. Kravchenko, coll. IS.

Genus *Atimia* HALDEMAN, 1847

Type species: *Atimia tristis* HALDEMAN, 1847 = *Clytus confusus* SAY, 1827 (monobasic - single reference)

One species occurs in the region dealt with in the present monograph: *Atimia nadezhdae* CHEREPANOV (?=*Myctus maculipunctus* SEMENOV et PLAVILSHCHIKOV). This is not the type species, and, moreover, one single larva available. The following description is therefore based on the following additional North American material (ex coll. U. S. National Museum, Washington): *Atimia confusa* (SAY) (type species, three larvae); *Atimia dorsalis* LECONTE (two larvae). All five larvae are mature, or praepupae. According to CRAIGHEAD (1923), larvae of these two species are almost indistinguishable. The larvae I have got from the Washington Museum are, on the contrary, distinctly different. This is very strange because it is very probably the same material (the collection number of *A. dorsalis* differs in one cipher - 4340g with the available specimens, 4240g in CRAIGHEAD, l. c., which looks like an error in one of the two cases, and the number of the available larvae of *A. confusa* is the same as one of the two numbers listed by CRAIGHEAD). Another curious point - the five available larvae are essentially devoid of microscopic spines, including pronotum. CRAIGHEAD (l. c.) mentioned large velvety pubescent (= microspiculate) area on the pronotum, but noted that »pubescence sometimes nearly obsolete«

(p. 35). The only one available half-grown larva of *A. nadezhdae* has these spines distinct. Analogically with some other Cerambycidae it could be preliminarily assumed that the spines are distinct in younger larvae and become obscure or absent in mature ones.

In addition, larvae of the Japanese *A. okayamensis* HAYASHI have been described (unfortunately in Japanese) and figured by KURODA (1977).

Body white, moderately elongate, in immature larvae distinctly broadened at prothorax, with very short thin almost unpigmented setae.

Head only moderately retracted (Fig. 28A showing the head somewhat unnaturally protracted), very broad, only slightly narrower than prothorax. Cranium strongly transverse (about 1.6–1.8), rather strongly depressed (about 2.2–2.4), only some ventral areas indistinctly microgranulate. Epicranium very poorly pigmented, with numerous stout recurved anterior setae, posterior two pairs of setae of dorsal rows usually much reduced or absent; sides abruptly roundly convex, in *A. dorsalis* even slightly angulate. Frontal lines ± distinct, narrow, almost straight except for short middle sections which are usually S-curved. Anteriorly frontal lines enter antennal openings and much weakened reach anterior cranial margin. Frons flat, smooth, may or may not be darker than epicranium. Four pairs of anterior frontal setae, other setae absent or very few. Epistomal margin gently sloping, broadly pigmented. Six epistomal setae, lateral pair at clypeal boundary, middle and medial pairs moved very far off from that line. Clypeus flat, abruptly tapering, basal half at most very finely pigmented, even anterior half almost not microreticulate. Labrum small, transversely oval, with broad basal pigmented band, anterior margin setose, two long isolated discal setae. Anterior epipharyngeal area devoid of setae, and with large area of very conspicuous microtrichia. Tormae very short, ± broadly triangular. Hind raised portion may bear two sclerotized strips. Gena from broadly pigmented (up to three times as wide as pleurostoma) to indistinguished from epicranium. One large but rather flat main stemma, pigment spot not very conspicuous, in some species almost absent, sometimes divided in two. Other stemmata absent. Hypostomal lines broad, remarkably diverging posteriorly, reaching postoccipital lines. Ventral sclerite (Fig. 28B) rather short (about 4.0–6.0), distinctly convex, mostly abruptly transversely raised, hind margin medially steeply to perpendicularly declivous, whole ventral sclerite, or at least its posterior angles, darker than epicranium. Metatentorial pits absent, metatentorium invaginated from border between ventral sclerite and membraneous collar, oblique, fully visible in ventral view. Gula moderately broad, gular lines raised, medial gular line very distinct, broadened anteriorly, reaching anterior margin. Usually about two pairs of setae.

Antennae moderately long, three-segmented, segments only finely pigmented. Second segment transverse, or at most as long as broad, third segment very long and slender, at least 2–3 times as long as broad, main sensillum extremely small, shortly conical, about as long as broad. Mandibular type I, mandible relatively slender, border zone at most slightly impressed, most of lateral face microreticulate. Apex and dorsal angle close to each other, blunt, rounded, cutting edge short, inner

face of apical portion concave, almost without keels. Basal portion with two lateral setae. Cardo relatively large, with distinct lateral seta. Stipes with complete basal band, ventral pigmentation of palpiger and mala indistinct, palpiger with short robust laterodorsal process. Palps short, robust, third segment elongate, about as long as second. Mentum feebly microreticulate, with continuous basal pigmented band. Pigmented areas of labial palpigers separate, palps short, second segment cylindrical, ligula short, broad (palps separate by about twice their width), two ventral setae, apical and dorsal margins covered with short microtrichia.

Prothorax short, broad (Fig. 28A). Pigmented band pale yellow, alar lobes unpigmented behind. Lateral furrows very distinct along whole length. Posterodorsal epipleural angle much reduced. Episternum sharply separated from lateropraesternum. Mediopraesternum poorly defined, anteriorly border line absent. Coxosternum separate, without pigmented spot. Microscopic spines from very distinct and widespread to nearly absent, even in same species. They may occur esp. on pronotum and adjacent regions of alar lobes (Fig. 28A), but on almost all other regions as well, and are rather long and slender, almost hair-like.

Meso- and metanotum mostly ± distinctly microspiculate, divided by inconspicuous X-shaped lines. Alar lobes distinctly protuberant. Mesothoracic spiracle small, shorter than (or rarely almost as long as) maxillary palps (which are rather short), weakly sclerotized, up to about 8–10 marginal chambers along upper margin. Transsternal lines distinct, lines dividing basisternum present, short. Indistinct micr. spines usually at lateral extremities of basisternum.

Legs moderately long, robust, femur and tibiotarsus very finely pigmented.

Abdomen with micr. spines mostly along intersegmental borders, on epipleurum etc., not on ampullae; latter non-granulate (or very poorly so), those of segments 4 to 6 remarkably different - deeply bilobed, each lobe strongly protuberant and moved laterad, so that these three segments are distinctly quadrangular (Fig. 27J). Dorsal ampullae with transverse lines inconspicuous (esp. on segments 4 to 6). Spiracles very broad (in some species circular), smaller than mesothoracic spiracle, finely pigmented, with a few relatively large marginal chambers at hind margin. Spiracles 1 and 8 larger than others. Pleural tubercles bearing 1–2 longer and a few shorter setae. Tubercles 7 and ± also 8 distinct. Transsternal line interrupted medially (very broadly on segments 4 to 6). Urogomphi sharp, robust, broadly separate (Fig. 27K), often incurved. Anal papillae small, sharply defined, bearing a few scattered short setae.

The genus is distributed in Nearctic and East Palaearctic (USSR, China, Mongolia, Japan) Regions. The whole genus, as fas as known, feeds exclusively in Cupressaceae, the two Palaearctic species whose bionomics are known feed in *Juniperus*.

Atimia nadezhdae CHEREPANOV, 1973

The single species occurring in the region dealt with. It has been synonymized with *A. maculipuncta* (SEMENOV et PLAVILSHCHIKOV, 1937) from Mongolia and

North China (LOBANOV, DANILEVSKY et MURZIN, 1981, p. 788). One single half-grown larva available which is characterized below:

Head well sclerotized, all setae slightly pigmented, relatively stout. Head has not been detached, width/length cranial ratio probably between 1.6 and 1.7. Frons and ventral sclerite much darker than epicranium, pigmentation of gena about three times as wide as pleurostoma. Epicranium roundly convex laterally. Each stemma with two contiguous pigment spots. Ventral sclerite abruptly raised, perpendicularly declivous behind, anterior margin broadly darkened, interrupted only by medial gular line. Second segment of labial palps almost as long as first. Prothorax with rather distinct microscopic spines on anterior margin, pronotum (Fig. 28A), epipleurum anteriorly, basal half of mediopraesternum, posterior angles of lateropraesternum, coxosternum, sternellar fold etc. All spiracles with two or three marginal chambers, abdominal spiracles circular. Certain abdominal areas do bear microscopic spines. Urogomphi not incurved, separated by about twice their length (Fig. 27K). (It is supposed that some of these characters will be found unstable, and will alter particularly in mature larvae - e.g. the extent of microscopic spines.) Length 6.5 mm. Generally the larva seems to be rather similar to the type species, *A. confusa*.

Host plant: *Juniperus*. According to CHEREPANOV (1979), larvae feed in dead branches of *Juniperus rigida*, about 1–25 cm in diameter, making separated galleries packed with frass between bark and wood. Pupation under bark or in surface wood layer. Pupae found in July to early August, adults appear in late July and August, emerge from the branch and hibernate (such true adult overwintering is rarely found in Cerambycidae). Eggs are laid next spring. One-year life-cycle. Almost identical habits revealed in Japanese A. *okayamensis* by KURODA (1977) who reports about feeding of adults on *Juniperus*-needles.

Distribution: Ussuri region, and, if the above synonymy is correct, Mongolia and North China.

Material: SU, Ussuri region, Zmeinaya Gora, 1/I, *Juniperus*, S. V. Murzin lgt., coll. IS.

Genus *Nothorhina* REDTENBACHER, 1845

Type species: *Callidium muricatum* DALMAN, 1877 = *Callidium punctatum* F., 1798 (monobasic)

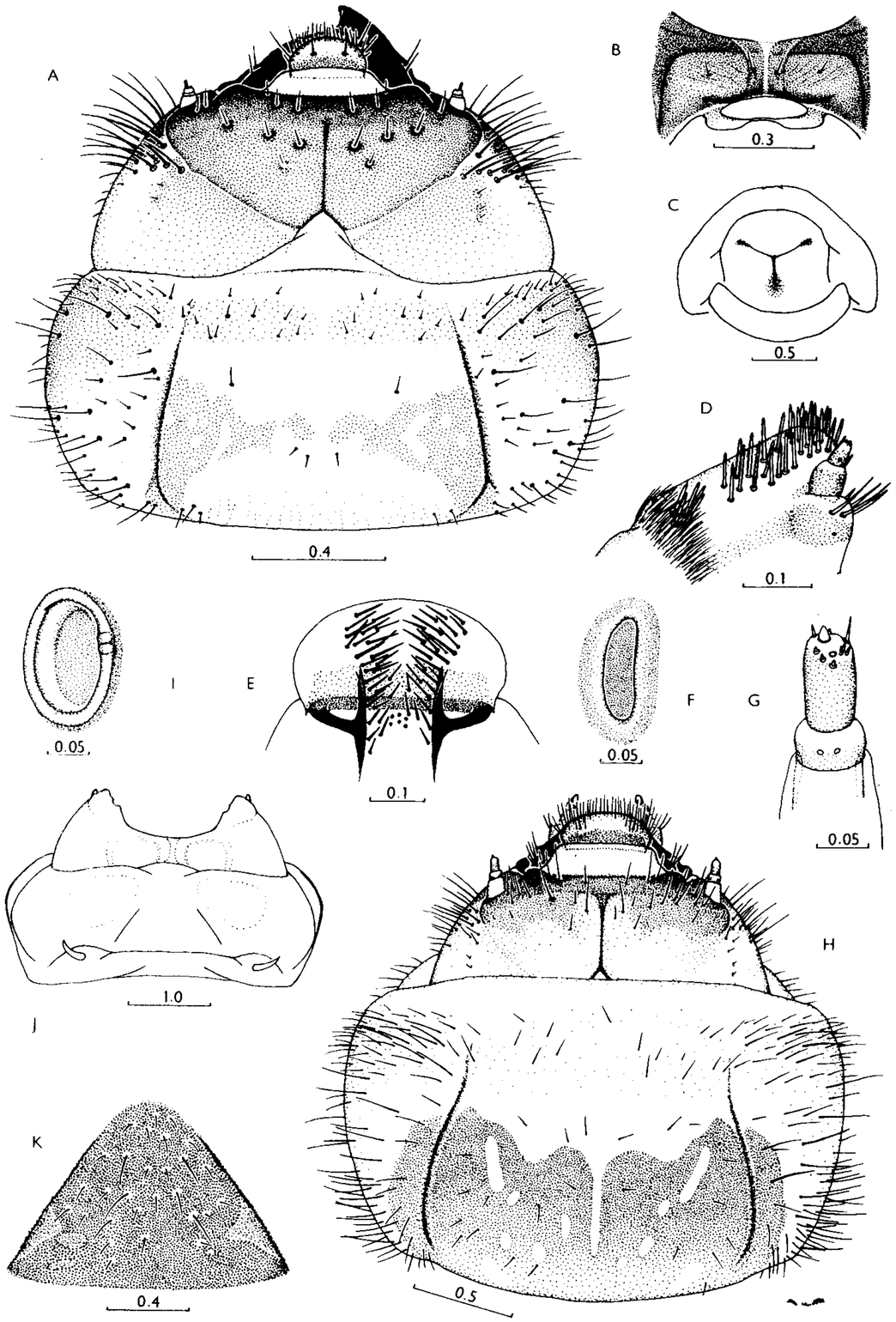
Body white, narrow and slender, with short sparse pale setae.

Head strongly retracted, much narrower than prothorax (Fig. 28H). Cranium moderately transverse (about 1.25–1.3), rather strongly depressed (2.1–2.3), poorly microgranulate, distinctly pigmented anteriorly, large posterior retracted part at most pale yellowish. Sides of epicranium moderately convex, broadly rounded, anterior epicranial setae moderately dense, short, not recurved, only two anterior pairs of setae of dorsal rows present. Frontal lines distinct, gently curved, broadly entering antennal openings and weakened reaching cranial margin. Frons flat, almost smooth, adfrontal (originally epicranial) setae rather distinct and shifted across frontal lines into frontal region. Frons with anterior one-third pigmented (usually excepting middle), pigmented area rather sharply bordered posteriorly. More than 1 + 4

stable pairs of frontal setae present, up to about 15 setae on each side. Epistomal margin broadly strongly sclerotized, moderately obliquely declivous. Usually about 8–12 (but in some specimens only 6) epistomal setae relatively close to clypeal border. Clypeus large, broad, moderately convex, strongly tapering, almost unpigmented, not microgranulate, sides gently emarginate. Labrum short, transversely oval, with broad strongly sclerotized basal band, numerous marginal and a few discal setae on anterior unsclerotized area. Tormae very characteristic, narrow, strongly sclerotized, with long anterior branch that makes them T-shaped (Fig. 28E). Two areas of numerous very stout epipharyngeal setae reaching almost to hind extremities of tormae. Gena broadly pigmented, about two times as wide as pleurostoma. Stemmata absent, or in young larvae pigment spots of main stemmata may be visible under cuticle - they are moved backwards in comparison with their usual position and become separated from pleurostoma. Hypostomal lines broad, almost not diverging, reaching postoccipital lines. Ventral sclerite flat, abruptly shortened (constricted) at middle (4.5–5.5), in later instar larvae distinctly darker than epicranium. Gula moderately broad, slightly raised and darkened, medial gular line distinct, broadened anteriorly, reaching anterior margin which is otherwise broadly heavily sclerotized. Metatentorial pits short, broadly distant from each other, very close to somewhat darkened hind margin. Metatentorium oblique, well visible in ventral view. Each hypostomal plate bearing about 6–10 setae.

Antennae long, deeply retractile, two-segmented (Fig. 28G). Segments distinctly pigmented, second longer than broad, main sensillum small, hardly longer than its basal diameter. Mandibular type I, mandible extremely variable in length, rather depressed, border zone indistinct, lateral face at most feebly microsculptured. Apical part with apex and dorsal angle blunt, rounded, close each other, dorsal angle may be strongly reduced. Two inner keels, often almost obliterated. Basal portion bearing several lateral setae, often arranged in transverse row. Submentum usually bearing two setae in hind half, each connecting lobe with up to 15 setae. Cardo extremely small, pushed laterad, closely resembling situation of Lamiinae, yet still separate and discernible, almost unpigmented, without seta. Stipes with basal band narrow laterally, palpiger long, with distinct yet narrow ventral pigmented band, process lacking. Mala extremely short and slender (about twice narrower than

Plate 28: A — *Atimia nadezhdae,* half-grown, head and prothorax, dorsal view. B — *A. nadezhdae,* half-grown, ventral sclerite. (Head has not been detached, metatentorium drawn as faintly visible through the membraneous collar, and as found in *A. dorsalis.*) C — *Nothorhina punctata,* mature, outline of abdominal segments 9 and 10 in posteroventral view, showing rudimentary urogomphi. D — *N. punctata,* mature, praelabium, lateral view. E — *N. punctata,* mature, diagrammatic illustration of tormae and epipharyngeal setae. (Drawn from an exuvia, it is therefore well visible that tormae are continuous with basal sclerotization of labrum. Microtrichia, labral setae etc. omitted.) F — *N. punctata,* mature, left abdominal spiracle. G — *N. punctata,* mature, left antenna, ventral view. H — *N. punctata,* mature, head and prothorax, dorsal view. I — *Tetropium castaneum,* mature, left abdominal spiracle. J — *T. gabrieli,* outline of cranium and prothorax, ventral view. (The smooth areas on lateropraesternum delimited by dotted lines.) K — *T. castaneum,* mature, prothoracic mediopraesternum.



rather broad first palpal segment), pigmented band indistinct. Palps short and robust, segments 2 and 3 of about equal length. Mentum not microreticulate, with complete or narrowly interrupted basal band. Pigmentation of labial palpigers broadly separate, palps rather long, second segment much shorter than first. Ligula narrow (palps separated by about one palp's width), covered with strong coarse setae, dorsal portion behind with a group of remarkably long microtrichia (Fig. 28D).

Prothorax (Fig. 28H) narrow, not remarkably transverse. Pigmented band nearly absent. Pronotum with very few short setae. Posterodorsal epipleural angle much reduced. Episternum separated from lateropraesternum. Mediopraesternum poorly defined, bearing about 10 setae. Coxosternum poorly separate from sternellar fold, latter medially very short and reduced. Coxal region with anteromedial pigmented spot. Microscopic spines widespread like in all Asemini: Sternellar fold, medial coxosternum, entire mediopraesternum, lateropraesternum along mediopraesternal line, certain areas of epipleurum and alar lobes, less distinct spines also elsewhere. Large area of particularly distinct spines includes posterior half of pronotum and narrow adjacent portions of alar lobes (Fig. 28H), smooth inclosed areas are sparse or almost absent (cf. e.g. with Figs 30D, 32A) except for usually one elongate oblique smooth area on each side.

Meso- and metanotum almost undivided, distinctly microspiculate. All body spiracles of about same size, with very characteristic broad as if »bent over« margins, no marginal chambers obvious from outer view (Fig. 28F). Transsternal lines obscure (more distinct in contracted larvae), short lines present dividing basisternum. Sterna microspiculate.

Legs comparatively short, robust, femur and tibiotarsus pigmented.

Ampullae completely microspiculate, dorsal transverse lines obscure. Spiracles - - see above in pterothorax. Pleural tubercles with two longer and a few shorter setae, tubercles 7 and 8 non-defined. Urogomphi extremely reduced (two minute contiguous unsclerotized tubercles at hind margin of ninth tergum, Fig. 28C), or absent (some authors - KEMNER, 1918, CHEREPANOV, 1979 - found urogomphi in some specimens more distinct). Anal papillae large and fused with anal segment (Fig. 28C), bearing numerous setae. Largest available larva 13 mm.

Two species known. However, the larvae and habits of the Indian *N. gardneri* PLAVILSHCHIKOV (GARDNER, 1942, DUFFY, 1968) seem to be at least transitional towards *Tetropium,* if not closer to the latter genus (two-three marginal chambers, acute urogomphi on joined base, larvae under bark of dead branches or trunks of *Pinus longifolia,* pupation in wood). However, the mesothoracic spiracle is not much larger than the abdominal ones, which character is closer to *N. punctata.* The North American »*Nothorhina*« *aspera* (LECONTE), once classified in that genus, belongs to the *Asemum*-group (one larva available), and is now classified in the genus *Megasemum* (see LINSLEY, 1962a).

Nothorhina punctata (F., 1798)

Host plant: *Pinus*. Habits rather unusual. Larva feeds in the bark of great living pines, often in solitary trees, or at least partly exposed to sunshine. Larvae feed in regions of moderately thick bark, making meandring ± separate galleries about the border of dead and living tissue. The trees can be usually recognized due to resin flow. There are usually only very few trees colonized, others are intact although apparently in the same situation. Pupation (as observed by me) in ± oblique cylindrical pupal cell in outer bark. Pupae in May to June (July), probably two-year development (in April, one evidently half-grown larva has been found, and one large larva found in early August).

Distribution: Europe, SW Siberia, Asia Minor. Very local throughout the range. Known also from Japan (if really conspecific with the West Palaearctic populations), but till now has not been found in continental East Asia. »South-West Himalayas« listed by HAYASHI (1979) applies evidently to *N. gardneri* (this latter species has been reported by earlier authors under *N. punctata*).

Material: 10. 5. 1964 CS, Bohemia, Suchdol n/Luž., 1/–, *Pinus,* M. Sláma lgt. et coll; 7. 8. 1977 CS, Bohemia, Chlum u Tř., 1/–, *Pinus,* lgt. et coll. S; 16. 4. 1983 CS, Bohemia, Třeboň, 5/I, *Pinus,* lgt. et coll. S.

Genus *Tetropium* KIRBY, 1837

Type species: *Tetropium cinnamopterum* KIRBY, 1837 (THOMSON design., 1864)

This genus is a junior synonym of *Isarthron* DEJEAN, 1835, but the generic name *Tetropium* has been used in all taxonomic papers, even if the author was aware of the synonymy (LINSLEY, 1962a). The International Comission on Zoological Nomenclature has been recently asked to suppress *Isarthron* (MROCZKOWSKI, 1986).

Type species of *Isarthron: Callidium aulicum* F., 1775 = *Cerambyx castaneus* L., 1758 (LINSLEY design., 1962).

The type species of *Tetropium* occurs in North America. Larvae are available (on loan from the U. S. National Museum, Washington, collection number 9734), and are covered by the following generic description. They are rather similar to the Palaearctic species available, differ from all of them e.g. by the form of urogomphi (Fig. 29G).

Body white, moderately elongate, distinctly broadened anteriorly, covered with relatively dense very short usually ± pigmented setae.

Head only moderately retracted, cranium broad, not much narrower than prothorax, distinctly transverse (1.4–1.6) and depressed (2.1–2.3), largely ± brightly pigmented, anterior half may be distinctly microgranulate. Epicranium pigmented except for lateral longitudinal pale band and areas adjacent to dorsal duplicated region (Figs 29B, C), pigmentation becoming gradually paler posteriorly. Sides moderately roundly convex, ± distinctly diverging posteriorly. Anterior region bearing ± numerous short often recurved setae, those lying in lateral pale area with distinct dark basal ring, latter in stronger setae usually somewhat raised. Dorsal rows may or may not be complete. Frontal lines very distinct, gently smoothly curved, rarely slightly S-curved, anteriorly passing through lower portion of antennal openings and much weakened reaching anterior cranial margin. Frons flat to

distinctly concave, darker than epicranium, may be distinctly obliquely rugose. Regular 1 + 4 frontal setae supplemented by a few shorter ones, in addition discal region of each frontal half with ± numerous scattered setiferous pores, each bearing a miniature seta. Epistomal margin broadly sclerotized, abruptly declivous, in some individuals pronouncedly step-like. Six (very rarely more) epistomal setae close to clypeal border. Clypeus broad, rather flat, abruptly tapering, feebly microreticulate, basal half very pale yellowish or reddish. Labrum strongly transverse, ± oval, basal half ferrugineous, anterior half unpigmented, its medial region glabrous, lateral regions and mainly anterior margin with stout setae, main discal pair usually indistinguishable from other setae. Epipharynx (Fig. 29A) with tormae almost transverse at base, then abruptly curved backwards. Anterior epipharyngeal setae very stout, fully separated from labral setae by glabrous marginal area. Gena intensively pigmented, becoming gradually paler posteriorly, not sharply delimited. Stemmata as in *Nothorhina,* pigment spots of main stemmata lying in anterior extremity of pale lateral area. Hypostomal lines broad, usually slightly diverging, reaching postoccipital line. Ventral sclerite very short at middle (about 4.0 to 6.0), usually darker than epicranium, gula moderately broad, raised, darkened, medial gular line somewhat variable but usually present and reaching anterior margin which is otherwise broadly strongly sclerotized. Hind margin ± darkened, too, metatentorial pits distinct, close to hind margin, closer to each other than in *Nothorhina* (each pit lies about middle of hind margin of its hypostomal plate). Metatentorium pointed obliquely inwards, visible in ventral view. Each hypostomal half with a few setae (up to 10–20 according to species).

Antennae short, three-segmented, segments finely pigmented, second slightly transverse, third small, at most slightly longer than broad. Main sensillum very small, about as long as broad. Mandibular type I, mandibles rather variable, typically short, robust. Border zone slightly impressed, not distinctly striate. Apical portion variable, apex and dorsal angle blunt, latter may be strongly reduced, cutting edge blunt, ± deeply emarginate, sometimes slightly angulate. Two low inner ridges present. Outer face may be shining or dull. Outer face of basal portion dull, microsculptured, bearing a few setae. Cardo very small, with conspicuous lateral seta. Pigmented bands of stipes and palpiger distinct, mala with only lateroventral pigmentation present. Palpiger long, without process, mala small, slender, much narrower than first palpal segment. Palps relatively short and robust, third segment moderately elongate to very stout, hardly as long as segment 2. Mentum finely microsculptured, basal band connected or very narrowly interrupted. Labial palpigers with their pigmented areas rather broadly separate, palps short, first segment large, second minute, hardly longer than broad. Ligula narrow (palps separated by slightly more than their own width), with ± conspicuous paired basal spots (occasionally connected by paler medial pigmentation), apical and dorsal margins bearing numerous stout setae.

Prothorax relatively short and broad. Pigmented band ± distinct, yellow,

rather broad, alar lobes sclerotized. Lower portion of alar lobes with distinct oblique impression (Fig. 11B). Posterodorsal angle of epipleurum extremely reduced and ± fused with alar lobe. Episternum completely fused with lateropraesternum. Mediopraesternum poorly defined anteriorly. Coxosternum almost fused with sternellar fold, latter with a pair of oblique impressions (Fig. 11B) which are secondary structures and must not be confused with border lines between coxosternum and sternellar fold. Coxal region with distinct pigmented spot. Most of prothoracic surface (except for sclerotized areas) covered with ± distinct microscopic spines (not continuous, with many small inclosed smooth areas, or distributed in smaller separate spots, esp. on lateropraesternum). Posterior half of pronotum with spines more distinct, usually blunt or turned into small sclerotized grains.

Meso- and metanotum microspiculate, divided by relatively distinct X-shaped lines. Mesothoracic spiracle large, at least as long as maxillary palp, broadly oval with rounded extremities, two small marginal chambers at upper extremity. Transsternal lines obscure, lines dividing basisternum short, distinct. Sterna non-granulate, microspiculate.

Legs much longer than maxillary palps, femur and tibiotarsus distinctly pigmented.

Ampullae poorly protuberant, almost not impressed medially, non-granulate, microspiculate, dorsal transverse lines obscure. Spiracles much smaller than mesothoracic one, with two small marginal chambers at posterodorsal margin (Fig. 28I), spiracles 1 and 8 larger than others. Pleural tubercles 7 and 8 essentially absent. Transsternal lines of ventral ampullae indistinct. Urogomphi present (may be absent in very young larvae of some species), brought together, often with joined base (Figs. 29D to G). Anal papillae moderately large, not very sharply separate from anal segment, bearing numerous short setae.

Larvae of five Palaearctic species available. They are relatively similar each other, and, moreover, rather variable. It would be therefore difficult to prepare a sharply exclusive species key, as practically all the characters overlap. However, comparing an undetermined larva (or, much better, a series of larvae) with the following differential diagnoses combined with distribution and host plant, it should be possible to identify species with reasonable certainity. If a character under certain species is followed by name of another species in brackets, then that character (as far as the available material allows to ascertain) seems to be particularly suitable for separating these two species. Young larvae are usually very hard to determine.

Tetropium castaneum (L., 1758)

Head setae relatively sparse, body setae relatively numerous, so that proepipleural setae usually distinctly denser than epicranial setae. Head pigmentation may be very dark, mouthframe occasionally dark brown to pitchy. Anterior region of cranium usually distinctly microreticulate or microgranulate (mostly at least anterior frontal angles, but often much of frontal area, gena, ventral sclerite) *(T. fuscum)*. Dorsal

epicranial pigment may or may not be spotted (cf. Figs 29B and C). Setae lying inside pronotal microspiculate area may be rather numerous and distinct (with conspicuous basal sclerotized ring). Micr. spines on lateropraesternum variable, from as in *T. fuscum* to as in *T. gabrieli*. Mediopraesternum in later instar larvae mostly with lateral yellowish spots, usually partly to completely devoid of spines (Fig. 28K). Urogomphi (Fig. 29F) mostly very close together, often converging, rarely almost fused, acute, borne on very distinct common protuberant base (usually less distinct in young larvae) *(T. gabrieli, T. gracilicorne)*. If they are much reduced (very rarely, Fig. 29F lower center), then it applies often to extremely large specimens where other characters are well developed. Length up to 27 mm, usually up to 25 mm.

Host plants: *Picea, Abies, Pinus,* according to CHEREPANOV (1979) also *Larix*. Larvae make flat irregular galleries filled with moderately coarse granular frass under bark of dead often relatively fresh trees, standing or fallen, occasionally in roots, mostly in stem. Pupation usually in the wood, in eliptical flat pupal cell at the end of a longer or shorter curved gallery filled with wood particles, but without a distinct »stopper« in the elliptical entrance hole. More rarely pupation occurs under bark. Usually two-year life-cycle, but the development pattern rathe variable, like in apparently all *Tetropium*-species. Larvae overwinter. Adults abundant in May to June.

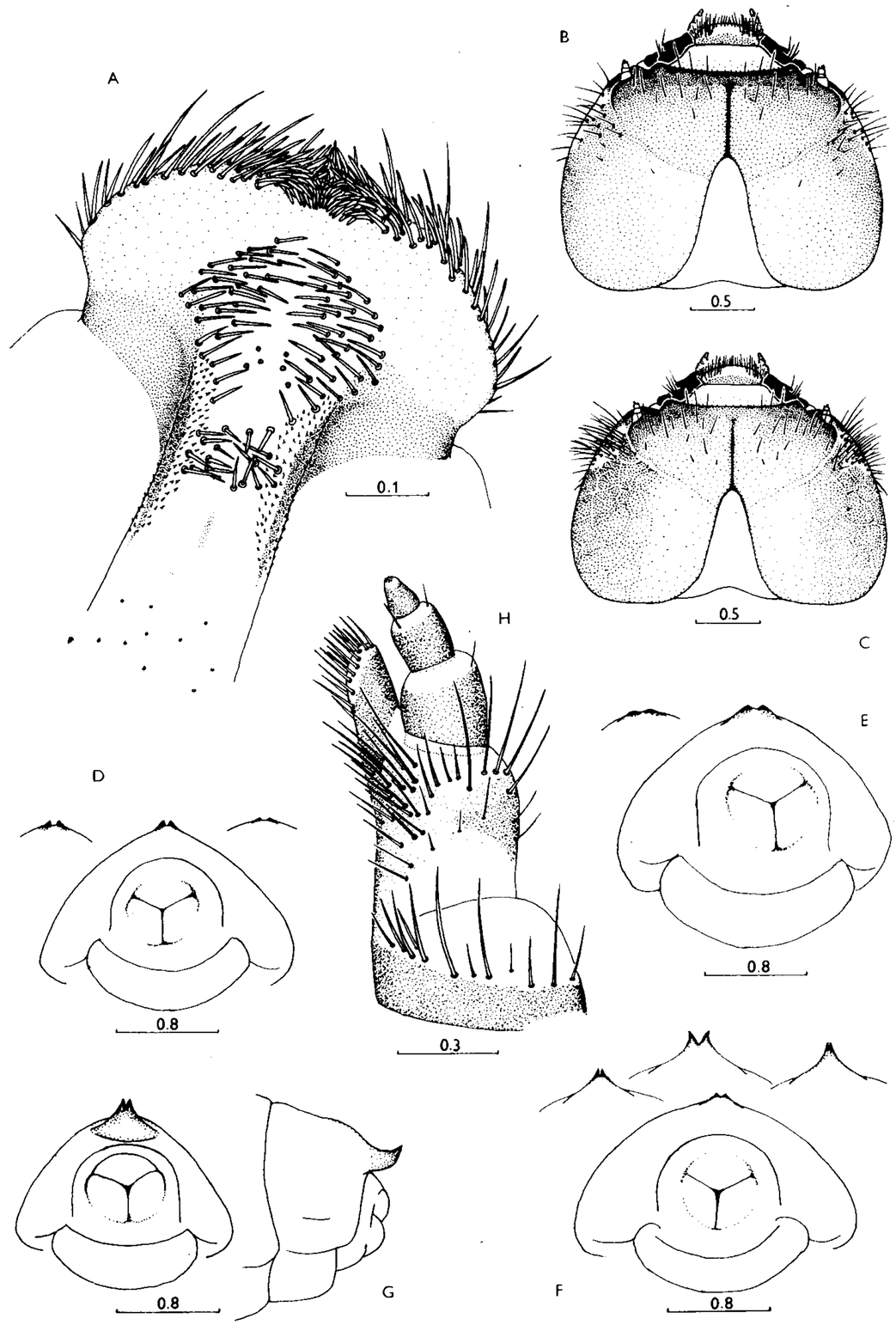
Distribution: Coniferous forests of most of cold and temperate Palaearctics, from Europe to Japan.

Material: CS, various spots, many larvae from *Picea* and *Abies,* lgt. et coll. M. Sláma and S; 17. 4. 1973 SU, Moscow region, Malinki, 1/I, *Picea,* N. B. Nikitsky lgt., coll. IS; 9. 6. 1972 SU, Tuva region, Ishtii-Khem, +/I, *Abies,* lgt. D, coll. IS; 21. 5. 1975 SU, Amur region, Kundur, 9/I, *Pinus,* lgt. D, coll. IS; 1. 10. 1972 SU, Kurile Islands, Kunashir, 7/−, *Picea,* B. M. Mamaev lgt., coll. IS.

Tetropium fuscum (F., 1787)

Setae about as in *T. castaneum,* epicranial setae in average sparser. Head pigmentation may be very dark. Anterior region of cranium very feebly microreticulate (usually except for epistomal margin), even anterior frontal angles ± shining, poorly microsculptured *(T. castaneum)*. Dorsal epicranial pigmented area continuous, or only marginally indistinctly spotted (Fig. 29B). Lateropraesternum entirely reticulately microspiculate, without large central smooth area (*T. gabrieli, T. gracilicorne*; apparently quite sharp difference, but the spines in *T. fuscum* are in some specimens very fine and poorly visible). Mediopraesternum without lateral yellowish spots, smooth areas absent or very small. Urogomphi mostly more distant than in *T. castaneum,* usually acute but short and ± without common protuberant base (Fig. 29D). Length up to 20 mm.

Plate 29: A — *Tetropium castaneum,* mature, epipharynx. B — *T. fuscum,* later instar, head, dorsal view. C — *T. gabrieli,* dtto. D — *T. fuscum,* outline of abdominal segments 9 and 10 in posteroventral view, showing urogomphi. E — *T. gabrieli,* dtto. F — *T. castaneum,* dtto. G — *T. cinnamopterum,* dtto. and lateral view. H — *Arhopalus rusticus,* later instar, left distal maxilla. lateroventral view.



Host plant: Picea, reliable found of this species in another host not known to me. Habits similar to the preceding species, pupation frequently under bark. However, the larvae can be only occasionally found together with *T. castaneum,* which indicates there are certain differences in habitat requirements.

Distribution: Europe, West Siberia.

Material: CS, various spots, 26/I, *Picea* (one my larva probably from *Abies*), lgt. et coll. M. Sláma and S; 7. 9. 1953 Sweden, Uppsala, 1/I, *Picea,* T. Palm lgt., coll. S.

Tetropium staudingeri PIC, 1901

Both head and body setae relatively dense. Cranium rather dark. Anterior region of cranium in later instar larvae moderately distinctly microreticulate. Dorsal epicranial pigment in available larvae not spotted. Lateropraesternum with microscopic spines about as in *T. fuscum*, in any case without large smooth central area. Mediopraesternum with at most small lateral smooth spots. Urogomphi always blunt, occasionally almost as reduced as in typical *T. gabrieli* and *gracilicorne* (small sclerotized tubercles), but usually slightly more prominent, with low common protuberant base. Largest available larva 23 mm.

Host plant: *Picea schrenkiana*. According to S. Bílý, the habits are similar to *T. castaneum*. Pupation in the wood.

Distribution: Mountains of Central Asia, incl. NW China. No one of the other four presently described species occurs in that region.

Material: 7. 7. 1976 SU, Kirgizia, Frunze, Ala Archa (2 100 m), 6/I, *Picea,* S. Bílý lgt., coll. National Museum, Prague; 4. 5. 1976 SU, Kazakhstan, Alma-Ata, 4/I, *Picea,* collector not stated, coll. IS; 21. 4. 1984 SU, Tyshkan, +/I, *Picea,* lgt. D, coll. IS.

Tetropium gabrieli WEISE, 1905

Head setae usually numerous (Fig. 29C), body setae in average sparser than in other species, so that epicranial and proepipleural setae of about same density. Head pigmentation never very dark, mouthframe at most dark ferrugineous. Anterior cranial region mostly poorly microreticulate. Dorsal epicranial pigmentation almost always broken into smaller separate spots in accordance with attachments of mandibular muscle streams (Fig. 29C). Pronotum with extremely sparse, short and indistinct setae. Lateropraesternum invariably with large central area on each side completely devoid of micr. spines (Fig. 28J, the area approximately marked out by dotted line) (*T. fuscum,* but see the note in the latter species). Mediopraesternum almost without lateral yellowish smooth spots. Urogomphi extremely reduced, low blunt tubercles on moderately protuberant common base (Fig. 29E) *(T. castaneum)*. Length up to 20 mm.

Host plants: *Larix,* very rarely others (*Pinus* - DUFFY, 1953). Habits similar to other species, larvae often also in thick branches, pupation frequently under bark. One-year development

apparently not infrequent. According to CRAWSHAY (1907, cited after DUFFY, l. c.), the larvae moult at least 7 times.

Distribution: Central Europe and some adjacent regions, reaching to Danmark, Germany, France, Great Britain.

Material: CS, Bohemia, various spots, many larvae from *Larix,* lgt. et coll. M. Sláma and S.

Tetropium gracilicorne REITTER, 1889

Very similar to *T. gabrieli,* differs by its distribution. Available larvae remarkable by almost unpigmented setae (and therefore hardly visible). In nearly all other available *Tetropium*-larvae the setae are at least pale ferrugineous. However, reliability of such colour character is doubtful. Microscopic spines are extremely fine and indistinct. Largest available larva 20 mm.

Host plants: *Larix* (much preferred), one available series taken from *Pinus sibirica*. Some of the hosts listed by MAMAEV and DANILEVSKY (1975) are doubtful, as some their larval material was possibly misidentified. Habits apparently similar to *T. gabrieli.*

Distribution: Siberia, Far East, Mongolia, China. Usually reported also for the Far East islans, but the eastern border of the range is not clear. I have seen no specimens from Kuriles, Sakhalin or Japan. CHEREPANOV (1979) has specimens from Ussuri region. It seems that the species has been occasionally misidentified, and the problem requires further study. HAYASHI (1979) listed *T. gracilicorne* for Japan, but the same author (in HAYASHI, MORIMOTO and KIMOTO, 1984) treats the Japanese populations as a separate species, *T. gracilicum* HAYASHI.

Material: June 1972 SU, Tuva region, Ishtii-Khem, 28/I (some series), *Larix* and *Pinus,* lgt. D, coll. IS; 5. 7. 1979 SU, lake Baikal, Irkutsk, fragments of one larva, *Larix,* lgt. et coll. S.

The *Asemum*-group

The larvae of the following genera are rather similar and it is advantageous to treat them together.

Genus *Asemum* ESCHSCHOLTZ, 1830

Type species: *Cerambyx striatus* L., 1758 (WESTWOOD design., 1840)

Genus *Arhopalus* SERVILLE, 1834

Type species: *Cerambyx rusticus* L., 1758 (WESTWOOD design., 1840)

Genus *Megasemum* KRAATZ, 1879

Type species: *Megasemum quadricostulatum* KRAATZ, 1879 (monobasic)

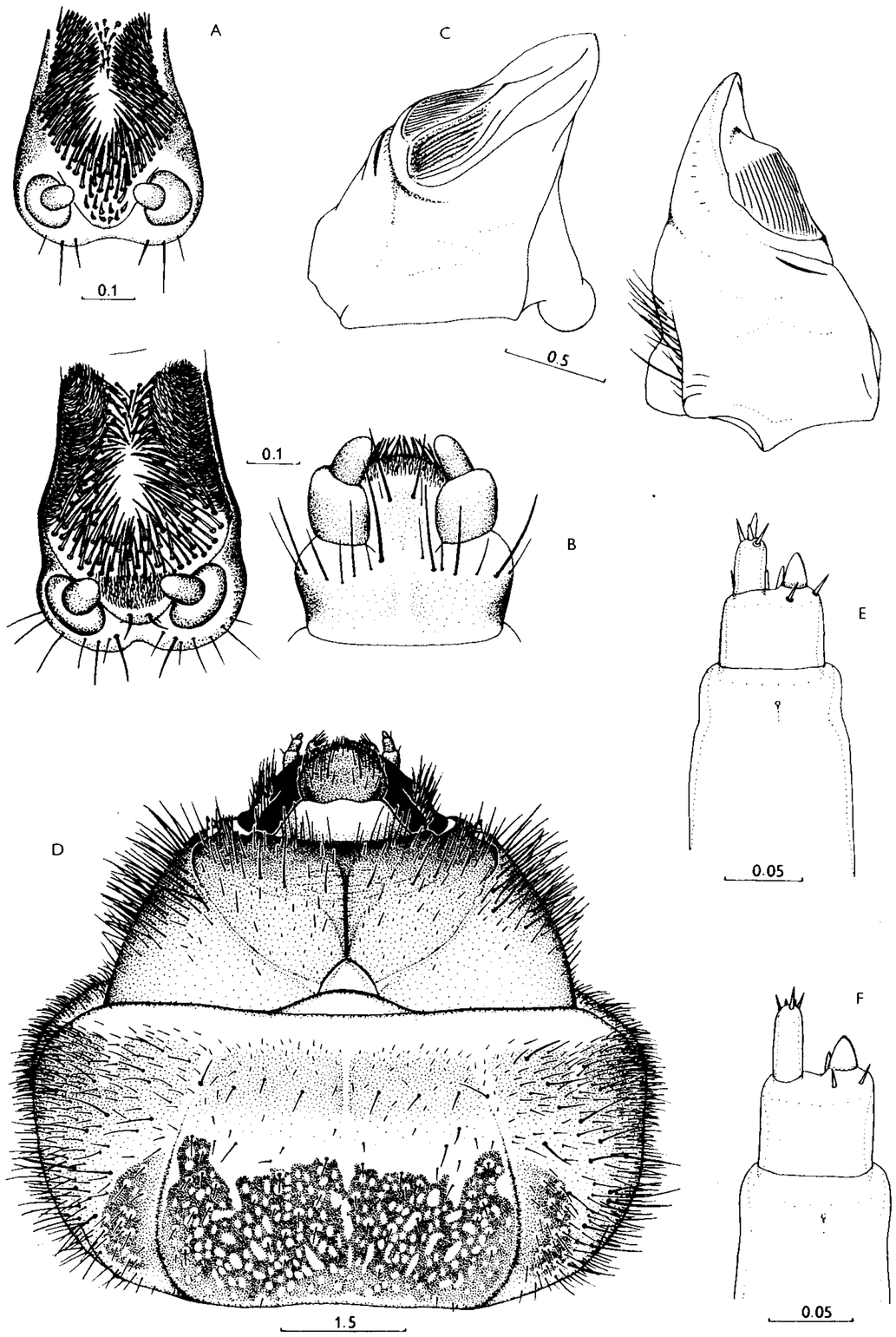
Genus *Spondylis* F., 1775

Type species: *Attelabus buprestoides* L., 1758 (monobasic)

Body robust, white or yellowish, distinctly broadened at prothorax, bearing moderately to very dense short ferrugineous setae (remarkably denser on some lateral regions of prothorax).

Head only moderately retracted. Cranium very broad, slightly narrower than prothorax, strongly transverse (1.4–1.6), distinctly depressed (2.0–2.3, in young larvae occasionally even more), some regions distinctly microreticulate. Sides diverging posteriorly, broadly roundly convex, anterior epicranial setae very numerous, ± recurved (Figs 30D, 31C). Dorsal rows may or may not be complete. Epicranium ± pale yellow. Frontal lines distinct, narrow, smoothly curved, rarely slightly S-curved, entering antennal openings, very indistinctly reaching anterior cranial margin. Frons flat, without remarkable macrosculpture, usually largely microreticulate. Always more than regular five pairs of frontal setae, particularly in anterior frontal angles. Frons besides it with ± numerous pores bearing miniature setae. Frontal region darker than epicranium, particularly in anterior half. Epistomal margin very dark, steeply obliquely to perpendicularly declivous to clypeus. In young larvae may be six epistomal setae, in later instars always more; main six setae close to clypeal border, some supplementary setae may be more distant from it. Clypeus relatively small, feebly convex, finely pigmented at base, often very distinctly microgranulate. Labrum flat, very long (Fig. 31B, in young larvae shorter, in young larvae of some species distinctly transverse, Fig. 31A), usually ± cordate, largely pigmented (basal half usually darker), apical margin pale, bearing numerous short setae, lateral and discal setae partly longer, sparse. Tormae short, broad at base, tapering, almost transverse, sometimes with indistinct anterior branch, medial extremity curved backwards. Anterior portion with two elongate setose areas (continuous with marginal setae of labrum, not separated from them - cf. *Tetropium*, Fig. 29A) which are broadly separate anteriorly and almost fused with each other posteriorly, thus inclosing an elongate oval glabrous area. Setae reaching ± far behind between tormae. Hind portion narrow, distinctly raised. Pleurostoma and gena always very distinctly microsculptured. Gena broadly pigmented (about two times as broad as pleurostoma), then becoming gradually paler, not sharply defined posteriorly (Fig. 31C). Stemmata in later instar larvae absent, in young larvae main stemmata ± visible, moved backwards, separated from pleurostoma by narrow sclerotized often somewhat protuberant area of gena. Hypostomal lines narrow, at most slightly diverging, reaching (Fig. 31C), or at least approaching (Fig. 31D) postoccipital line. Ventral sclerite rather long (about 2.0–3.0 in later instar larvae, in young larvae may be shorter), darker than epicranium except in very young larvae. Anterior margin dark, strongly sclerotized, at most narrowly medially

Plate 30: A — *Asemum striatum*, later instar, praelabium, anterior view. B — *Spondylis buprestoides*, half-grown, dtto. and ventral view. C — *Arhopalus rusticus*, mature, left mandible, dorsal (right) and medial (left) views. D — *Arh. rusticus*, submature, head and prothorax, dorsal view. E — *Asemum striatum*, later instar, left antenna, dorsal view. F — *Arhopalus tristis*, later instar, dtto.



interrupted by medial gular line. Gula very narrow, mostly with ± raised gular lines, medial gular line from distinct to obsolete, may (Fig. 31C) or may not (Fig. 31D) reach anterior margin. Hind margin gently emarginate, metatentorial pits short, well separate from hind margin. Metatentorium projecting strongly inwards, poorly visible or invisible in ventral view. Ventral sclerite bearing numerous setae.

Antennae very short, three-segmented (Figs 30E, F), segments cylindrical, sclerotized. Segment 2 about as long as broad, segment 3 slender, at least slightly longer than broad (except for youngest larvae), longer (occasionally several times) than small main antennal sensillum. Mandibular type II (only in youngest larvae sometimes with type II-keel much reduced or almost absent). Mandible short, robust (Fig. 30C), border zone gently impressed, not striate. Apical part with apex produced, sharp, dorsal angle short, two distinct inner keels running close together, type II-keel with distinct dorsal and ± distinct inner striated plates. Outer face shining or microsculptured. Outer face of basal portion always microreticulate, dull, bearing unusually numerous setae arranged in transverse recurved zone. Labiomaxillary complex (Fig. 31C) relatively similar to *Tetropium*. Submentum and connecting lobes in later instar larvae finely pigmented. Cardo extremely small, bearing one or even several lateral setae. Maxilla (Fig. 29H) slender, mala with pigmented band ± complete, palps long and slender, segment 1 very large, segment 3 slightly to twice shorter than segment 2. Mentum finely distinctly microgranulate, dull, with broad uninterrupted basal band. Lateral sclerotized praelabial band reaching ± only on lateral face of labial palpigers, their ventral face only finely incompletely pigmented. Palps relatively long, first segment large, second small, short. Ligula moderately broad, may have ventral pigmented spot, apical and dorsal portion bearing dense stout setae (Fig. 30A, rather modified pattern combined with microtrichia found in *Spondylis*, Fig. 30B).

Prothorax short, broad. Dorsal pigmented band ± distinct, pale yellow to yellow-orange. Posterior half of pronotum and small regions of alar lobes microspiculate (Fig. 30D), their spines more distinct and larger than those on other body areas. Alar lobes and epipleurum anteriorly with remarkably numerous setae, some of them may be very short and stout, almost spine-like. Alar lobes with distinct oblique furrows like in *Tetropium*. Posterodorsal epipleural angle much reduced, epipleurum anteriorly with distinct pigmented spot. Episternum completely fused with lateropraesternum. Mediopraesternum ± defined (very poorly at apex), bearing numerous setae. Coxosternum separate from sternellar fold, coxal region with distinct pigmented spot. Microscopic spines on mediopraesternum, narrow neighbouring areas of lateropraesternum, and on anterior half of sternellar fold.

Meso- and metanotum microspiculate, divided by not very distinct X-shaped lines. Mesothoracic spiracle large, at least as long as maxillary palp, posterodorsal margin with variable number of marginal chambers (up to about 30 in *Megasemum*); occasionally they are very small and hardly visible. Transsternal lines extremely reduced, incomplete, composed of a few separate fine smooth impressions. Lines

dividing basisternum are reduced to short oblique deep impressions at medial coxal extremities. Sternum non-granulate, largely microspiculate.

Legs relatively long and slender, femur and tibiotarsus at least finely pigmented, former with rather numerous subapical setae from inner side.

Ampullae not much protuberant, broadly very shallowly impressed along midline, non-granulate, completely covered with micr. spines. Two dorsal and one ventral pairs of lateral impressions present, both dorsal and ventral transverse lines ± absent (Fig. 32B). Abdominal spiracles much smaller than mesothoracic one, hind margin with several small marginal chambers (often two in young larvae), spiracles 1 and 8 larger. Pleural tubercles present on segments 1 to 8, but tubercles 7 and 8 poorly developed; tubercles bearing greater variable number of setae. Urogomphi present (may be absent in youngest larvae), of various shapes (Figs 32C to J). Anal papillae moderately large, ± separate from anal segment, bearing varying number of short setae.

The larvae of the subgenus *Cephalocrius* SHARP, 1905, differ substantially from those of *Arhopalus* s. str., and, as long as *Megasemum, Arhopalus* and *Asemum* are considered separate genera, it should be perhaps also given generic rank.

Key to genera and species of the *Asemum*-group

1(2) Ligula with ventral setae separated from those on dorsal face by a broad band of long distinct microtrichia (Fig. 30B). Urogomphi very broadly separate (Fig. 32D) (*Spondylis* F., 1775, characters do not hold for the North American *S. upiformis* - see note in close of the *Asemum*-group) . . . . . *S. buprestoides*

2(1) Ligula with ventral setae at most indistinctly separate from remaining ones, microtrichia absent (Fig. 30A). Urogomphi closer together (Figs 32C, E to J).

3(4) Urogomphi fused and bifurcate apically, pointed caudad, their base remarkably convex (Fig. 32H) (*Arhopalus* sg. *Cephalocrius* SHARP, 1905) . . . . . *Arh.* (*C.*) *syriacus*

4(3) Urogomphi ± separate, in natural position pointed obliquely upwards.

5(6) Head strongly sclerotized, anterior and posterior margins of ventral sclerite dark, their pigmentation not interrupted (at most constricted in young larvae) by medial gular line. Setae very dense, stout, ferrugineous, prothoracic anterior praesternal lobe bearing dense minute setae, particularly in mature larvae (Fig. 31D) (*Megasemum* KRAATZ, 1879, characters do not hold for the North American *M. asperum*) . . . . . *M. quadricostulatum*

6(5) Dark pigmentation of anterior and posterior margins of ventral sclerite always interrupted by medial gular line (Fig. 31C). Setae on anterior praesternal lobe sparser to absent (Fig. 31E).

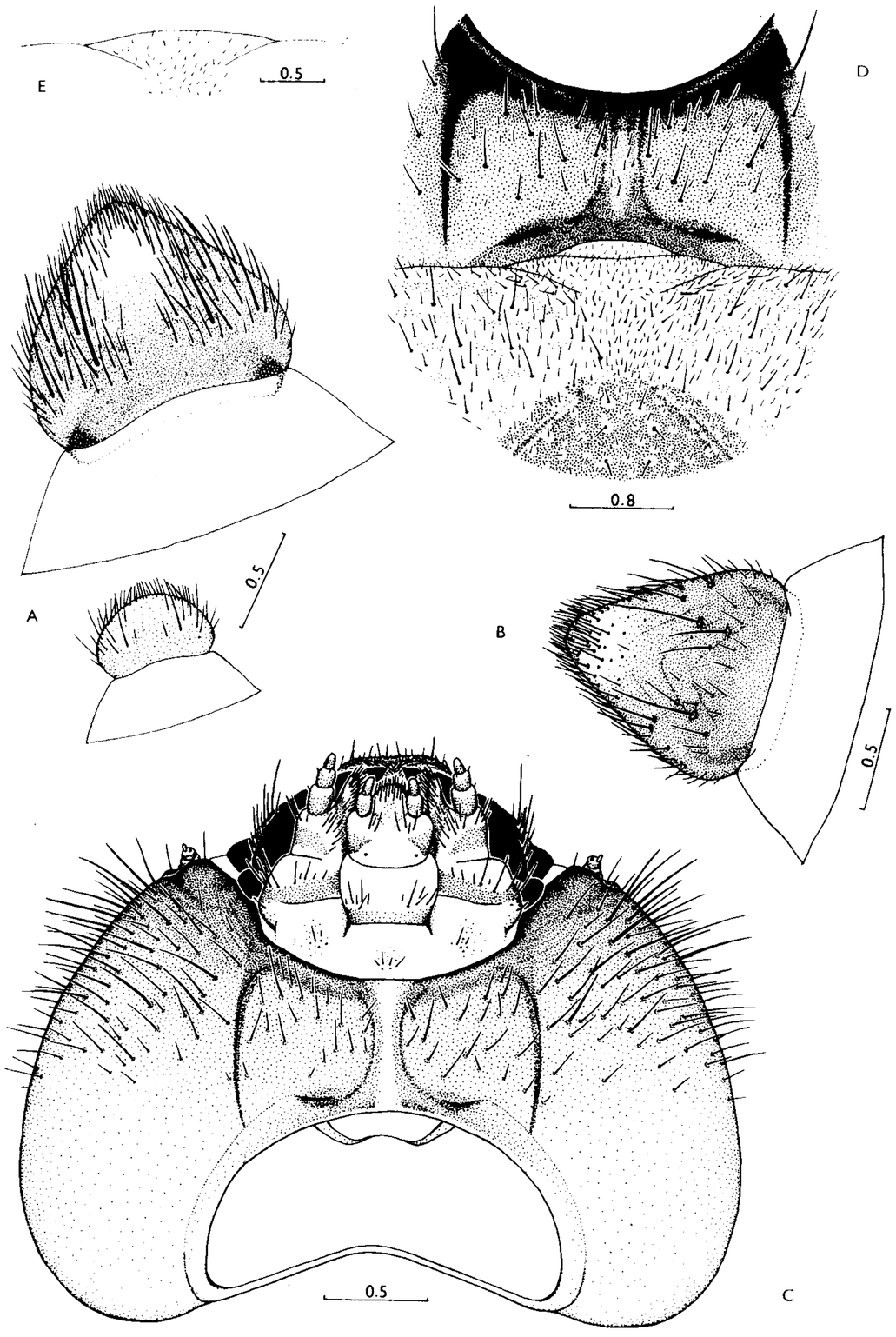
7(12)! Posterior frontal half almost not microreticulate, shining. Pronotal microspiculate area with smooth spots relatively few and large (Fig. 32A), spines finer, less distinct. Main antennal sensillum relatively slender, much narrower than third segment, distinctly longer than broad (Fig. 30E). Urogomphi as figured (32E to G) (*Asemum* ESCHSCHOLTZ, 1830).

8(9) Urogomphi small, broadly separate, usually as if slightly curved against one another . . . . . *As. punctulatum*

9(8) Urogomphi larger, closer together, robust, fleshy.

10(11) Urogomphi shorter, stout, conical, not curved (Fig. 32F) . . . . . *As. striatum*

11(10) Urogomphi long, slender, curved (Fig. 32G) . . . . . *As. tenuicorne*



12(7)! Posterior frontal half distinctly microreticulate (poorly so in young larvae of *Arh. tristis*), dull. Microscopic spines coarser, more distinct, pronotal area with numerous small smooth spots (Fig. 30D, slightly less numerous in *Arh. tristis* and *pinetorum*). Main antennal sensillum more robust, at most very slightly longer than broad (Fig. 30F). Urogomphi as figured (32I, J) (*Arhopalus* SERVILLE, 1834).

13(14)! Apical sclerotized portions of urogomphi distinctly flattened, urogomphi usually more widely separate (Fig. 32I). Smooth spots on pronotum fewer, their total area relatively smaller. Anterior praesternal lobe bearing at most very few minute setae . . . . . *Arh. tristis, pinetorum*

14(13)! Apical parts of urogomphi conical, not flattened, urogomphi usually closer together (Fig. 32J). Microspiculate pronotal area with numerous smooth spots occupying relatively larger area (Fig. 30D, less numerous in young larvae). Anterior praesternal lobe in mature larvae bearing relatively numerous short setae (Fig. 31E) . . . . . *Arh. rusticus*

Spondylis buprestoides (L., 1758)

Cranium slightly more transverse than in other species (about 1.6). Epistomal margin abruptly perpendicularly declivous, particularly about middle. Basal sclerotized half of clypeus almost not microreticulate. Labrum in mature larvae about as long as broad, in younger larvae remarkably shorter, broadly rounded (Fig. 31A). Ventral sclerite relatively short, in mature larvae about 2.7, in young larvae often far over 3. Hypostomal lines seldom fail to reach postoccipital line. Gula not raised or darkened, medial gular line not very distinct, hardly reaching anterior margin, but anterior dark pigmentation always interrupted by paler medial zone. Main antennal sensillum usually slightly longer than broad, third segment short, occasionally not longer than broad, very seldom as much as twice longer, at most slightly overreaching main sensillum. Third segment of maxillary palp in mature larvae almost twice shorter than second (in young larvae relatively longer). Ligula with a few (often two) ventral setae separated from dorsal setae by large area covered with microtrichia, dorsal labial portion also with large lateral areas covered with microtrichia (Fig. 30B). Ligula with large ventral sclerotized spot.

Setae moderately dense, prothoracic anterior praesternal lobe glabrous. Microscopic spines moderately distinct, microspiculate area of pronotum with very few small indistinct smooth spots. Mediopraesternum usually with ± large medial smooth area, lateral microscopic spines much more distinct than medial ones. According to DUFFY (1953) who had larvae from western Europe, spines of mediopraesternum may be fully divided into two separate areas. Marginal chambers relatively large, distinct, up to about 15 chambers in mature larvae. Urogomphi small, sharp, very broadly separate (Fig. 32D), in young larvae, however, mostly blunt, often almost unsclerotized tubercles. Length up to 32 mm.

Plate 31: A — *Spondylis buprestoides,* labrum of mature (upper) and young (lower) larva. B — — *Megasemum quadricostulatum,* mature, labrum. C — *Asemum striatum,* later instar, head, ventral view. D — *Megasemum quadricostulatum,* mature, ventral sclerite and anterior region of prothoracic praesternum, ventral view. E — *Arhopalus rusticus,* mature, prothoracic anterior praesternal lobe.

Host plant: *Pinus*. I have not found reliable record of another host. Larvae live in dead trees or in stumps, almost always underground, or at least at the ground level. Young larvae under bark, older larvae mostly entering the wood (according to the degree of decomposition). The galleries are often initiated in roots at a distance from the stem. According to CHEREPANOV (1979) the females are capable of digging and lay eggs directly on the root surface. Several-year life-cycle. Pupation in spring/summer in the wood (often at the stem base), flight in summer. Similar larval habits have been found in the North American *S. upiformis* MANNERHEIM (GARDINER, 1970a) feeding in *Picea glauca*.

Distribution: Largely distributed in coniferous forests of most of Palaearctic Region, from Europe to Japan.

Material: CS, various spots, 39/I, *Pinus*, lgt. et coll. M. Sláma and S; 18. 5. 1959 SU, Tartarian ASSR, Buinsk region, one larva, collector not stated, coll. IS.

Megasemum quadricostulatum KRAATZ, 1879

Head rather brightly pigmented, mouthframe very dark, frons and ventral sclerite in later instar larvae much darker than epicranium. Cranium less transverse (about 1.5). Epistomal margin abruptly declivous. Clypeus entirely distinctly microreticulate. Labrum very long, in mature larvae may be slightly longer than broad, cordate, acutely tapering anteriorly (Fig. 31B). Ventral sclerite moderately long (about 2.5 in later instar larvae). Hypostomal lines in later instar larvae usually fail to reach postoccipital lines. Gula raised, mostly bearing several setae (in other species usually glabrous). Medial gular line much reduced, reaching neither anterior nor posterior margin which are both very dark (Fig. 31D). Main antennal sensillum relatively small, about as long as broad, third segment long, slender, more than twice as long as broad, far overreaching main sensillum. Third segment of maxillary palp in later instars much (almost twice) shorter than second. Ligula with ventral setae not separated from dorsal ones by area of microtrichia, large ventral sclerotized yellowish spot present.

Setae ferrugineous, extremely dense, in mature larvae almost all body surface covered (in addition to usual setae) with dense rather regularly distributed short setae, latter are very dense also on prothoracic anterior praesternal lobe (Fig. 31D). Microscopic spines ferrugineous, very distinct, pronotum with smooth spots small and in average even slightly more numerous than in *Arhopalus rusticus* (cf. Fig. 30D), also other microspiculate areas in mature larvae with less conspicuous small inclosed smooth spots. Mediopraesternum without larger medial smooth area. Marginal chambers small, very numerous (up to about 25–30). Urogomphi relatively short, robust, distinctly flattened, blunt (Fig. 32C). Largest available larva 40 mm.

Bionomics (CHEREPANOV, 1979): Larvae in *Abies*, also in *Pinus* and *Picea*, in dead standing or fallen trees, initially under bark, later in the wood where also pupation occurs in late spring and summer. Flight in summer, extended till September. Development period not given, but undoubtedly at least two or more probably three years.

Distribution: Far East - Amur, Ussuri, NE China, Korea, Far East islands.

Material: September 1972 SU, Kurile Islands, Kunashir, Mendeleevo, 15/I, *Abies*, lgt.

A. V. Kompantsev and D, coll. IS; 15. 5. 1967 SU, Ussuri region, Suputinka, 1/I, *Pinus*, B. M Mamaev lgt., coll. IS.

Arhopalus (Cephalocrius) syriacus (REITTER, 1895)

Cranium rather pale, mouthframe dark ferrugineous, frons and ventral sclerite occasionally almost not darker than epicranium. Epistomal margin relatively low, may be abruptly declivous, but very often only obliquely roundly sloping. Clypeus ± microreticulate (basal half feebly so, sometimes almost smooth). Labrum long, cordate, even in very young larvae almost as long as broad. Ventral sclerite relatively short (about 2.5–3.0 in later instar larvae, often far over 3 in young larvae). Hypostomal lines reaching postoccipital line. Gula very feebly raised, medial gular line inconspicuous, hardly reaching anterior margin. Main antennal sensillum at most slightly longer than broad, third segment usually about twice as long as broad, far overreaching main sensillum. Third segment of maxillary palp almost twice shorter than second. Ligula with ventral setae not separated from dorsal ones, ventral sclerotized spot ± absent.

Setae relatively dense, anterior praesternal lobe bearing at most very few scattered minute setae, in young larvae glabrous. Microscopic spines distinct, pronotum with smooth spots distinct, less numerous than in *A. rusticus* (cf. Fig. 30D). Mediopraesternum without medial smooth area. Marginal chambers few, very small, up to about 10 chambers present. Urogomphi rather peculiar (Fig. 32H). Largest available larva 30 mm.

Bionomics: According to M. Sláma (personal communication), the habits are very similar to other *Arhopalus*-species.

Distribution: Apparently the whole Mediterranean area; Canary Islands.

Material: June 1984 Greece, Creta, Omalos, 7/I, *Pinus*, M. Sláma lgt. et coll; 30. 6. 1969 France, Alpes Maritimes, Le Muy, 7/–, *Pinus*, M. Sláma lgt. et coll; Tunis, La Kesra, 1/I, *Pinus halepensis*, M. Sláma lgt. et coll; 4. 1. 1972 Canary Islands, Teneriffa, Agua Manza, 2/I, *Pinus canariensis*, T. Palm lgt., coll. S; 13. 5. 1973 Spain, Valldoreix, 1/–, *Pinus*, F. Español lgt., coll. E. Vives.

Arhopalus (s. str.) *rusticus* (L., 1758)

Cranium rather intensively pigmented, in later instar larvae with distinct orange--ferrugineous tone. Epistomal margin of variable shape, roundly or steeply declivous. Clypeus roughly microgranulate. Labrum long, cordate, only in very young larvae broadly rounded and slightly shorter than broad. Ventral sclerite long (up to 2.2 in mature larvae). Hypostomal lines with very rare exceptions reaching postoccipital line. Gula ± raised, gular lines not, or at most very finely darkened. Medial gular line may or may not reach anterior margin, but dark anterior pigmentation always interrupted by paler medial zone. Main antennal sensillum rather short, about as long as broad, third antennal segment in later instars usually at least twice as long

as broad, far overreaching main sensillum. Third segment of maxillary palps very short, in later instars often twice shorter than segment 2 (in young larvae relatively longer). Ligula continuously setose, with at most small indistinct ventral pigmented spot.

Setae relatively dense, anterior praesternal lobe in young larvae almost glabrous, in older and esp. mature ones bearing relatively numerous short setae (Fig. 31E). Microscopic spines very distinct, ferrugineous, pronotum with numerous small distinct smooth spots (Fig. 30D). Mediopraesternum without larger medial smooth area. Marginal chambers few, very small, up to about 10–14 (rarely more than 8) chambers present. Urogomphi (Fig. 32J) small, close together, sharp (rarely somewhat blunted), conical, not flattened, large apical portions sclerotized. Length up to 35 mm.

Host plants: *Pinus*, more rarely *Picea, Abies, Larix*. Larvae in dead trees, in stems of greater diameter (fallen or standing, then not too high above ground level), or in stumps, often penetrating into surface roots (but eggs are not laid on roots). Even if eggs are laid higher on the stem, the larvae often die due to the dead tree often soon losing its bark which causes dessication of the wood higher above ground level. Young larvae under bark, soon penetrate into the wood where also pupation occurs in spring/summer. Flight in summer. At least two- or three-year development.

Distribution: Coniferous forests of most of Palaearctic Region. Proper status of some North American taxa assigned as subspecies to *A. rusticus* (LINSLEY, 1962a) needs, in my opinion, further study.

Material: Many larvae from Spain, Greece, CS, SU (Krasnodar region, lake Baikal, Ussuri region, Kurile Islands), taken from *Pinus, Picea, Larix,* in collections of M. Sláma, E. Vives, IS, S. Adults reared from many of these series.

Arhopalus (s. str.) *tristis* (F., 1787) [= *ferus* (MULSANT, 1839)]

Similar to *A. rusticus*. Urogomphi always fully separate, larger, their apical sclerotized portions always flattened (Fig. 32I). Smooth spots inclosed in microspiculate area of pronotum are slightly less numerous and occupying relatively smaller area. Mediopraesternum often with larger basal medial smooth area. Anterior praesternal lobe with at most very sparse setae. Clypeus not so distinctly microsculptured. Main antennal sensillum in average slightly longer (Fig. 30F). Marginal chambers more numerous, more than 10 chambers are not infrequent. Hypostomal lines may or may not reach postoccipital line. Maximal length about the same as in *A. rusticus*.

Host plants: *Pinus, Picea*. Habits apparently similar to *A. rusticus*. According to DUFFY (1953), larvae prefer lower part of stem and exposed roots, and are often found together with *Asemum striatum*.

Distribution: Coniferous forests of most of Palaearctic Region, but apparently more local, not as widespread as the preceding species. Absent from Japan and other Far East islands.

Material: 30. 6. 1969 France, Alpes Maritimes, Le Muy, 6/I, *Pinus*, M. Sláma lgt. et coll; six larvae from Great Britain, no other data available, but apparently they are a portion of the material cited by DUFFY (1953), coll. British Museum; 8. 4. 1979 SU, Crimea, Simferopol env., Vodokha, 4/–, *Pinus*, lgt. A. F. Bartenev, coll. IS.

Arhopalus (s. str.) *pinetorum* (WOLLASTON, 1863)

In the two available mature larvae, no differences were found from *A. tristis*.

Host plants: *Pinus canariensis, P. insignis*. Larvae in moist decaying stumps and stems (DEMELT, 1974). Habits undoubtedly similar to other *Arhopalus*-species.

Distribution: Canary Islands.

Material: Canary Islands, Teneriffa, Agua Manza, 2/I, *Pinus canariensis*, T. Palm lgt., coll. S.

Asemum striatum (L., 1758)

Head and body pigmentation with reddish tone, rather pale, frons and ventral sclerite at most slightly darker than epicranium. Posterior frontal half almost not microreticulate, shining. Epistomal margin relatively low, not too abruptly declivous. Basal sclerotized half of clypeus usually poorly microreticulate. Labrum long, cordate, in young larvae moderately transverse. Ventral sclerite long (about as in *Arhopalus rusticus*). Hypostomal lines distinctly reaching postoccipital line. Gula raised, gular lines mostly ± darkened even in very young larvae. Medial gular line usually does (seldom does not) reach anterior margin, but always interrupting anterior dark pigmentation by paler medial zone. Main antennal sensillum slender, distinctly longer than broad, distinctly narrower than segment 3 (Fig. 30E). Third antennal segment in later instar larvae usually long, about 1.5–2 times as long as broad, overreaching main sensillum. Third segment of maxillary palp even in mature larvae usually only moderately shorter than second, in any case never twice shorter. Ligula with continuous setal cover, and with at most indistinct diffuse often V-shaped ventral spot.

Setae relatively sparse, anterior praesternal lobe essentially glabrous. Microscopic spines finer, pronotum with relatively few smooth spots inclosed in microspiculate area (Fig. 32A). Mediopraesternum usually without larger medial smooth area. Marginal chambers very few (rarely more than six chambers present), small. Urogomphi (Fig. 32F) large, robust, fleshy, conical or moderately flattened, ± blunt, ± abruptly constricted and sclerotized at tip. Length up to 26 mm.

Host plants: *Pinus* (preferred), *Picea, Abies, Larix*. Habits generally similar to *Arhopalus*-species, but the larvae distinctly prefer sites at ground level and surface roots. May be found also in trees or stumps of smaller diameter which are rarely inhabited by species of *Arhopalus*.

Distribution: Coniferous forests of cold and temperate Palaearctics, absent from warmer southern regions; North America.

Material: CS, Hungaria, Bulgaria, SU (Caucasus, lake Baikal, Amur region, Sakhalin), many larvae from *Pinus* and *Larix*, coll. M. Sláma, IS, S (adults reared from many series).

Note: *Asemum amurense* KRAATZ, 1879, has been synonymized with *A. striatum* (LOBANOV, DANILEVSKY et MURZIN, 1981). Also CHEREPANOV (1979) noticed that the two supposed species are indistinguishable, and treated *amurense* as a subspecies of *striatum*, which cannot be accepted since they occur sympatrically, with all transitional forms.

Asemum punctulatum BLESSING, 1872

Very similar to *A. striatum*. Differs conspicuously by the form of urogomphi (Fig. 32E).

Bionomics (CHEREPANOV, 1979): Larvae found in *Pinus coraiensis*. Eggs laid on dying stems, larvae initially under bark, then (in the second year) in surface wood layers. Pupation in May to June in the wood, flight in summer. Two-year life-cycle. The species does not show the pronounced tendency of *A. striatum* to feed at ground level or underground.

Our material shows that the species is apparently polyphagous on various conifers.

Distribution: Amur - Ussuri region, NE China, Korea, Far East islands incl. Japan.

Material: 1972 - 77 SU, Kurile Islands, Kunashir, Mendeleevo, +/I (some series), *Picea, Pinus, Abies,* lgt. B. M. Mamaev, A. V. Kompantsev and D, coll. IS; 1964 - 69 SU, Ussuri region, Suputinka nature reserve, 6/—, *Pinus,* collector not stated, coll. IS.

Asemum tenuicorne KRAATZ, 1879

Very similar to *A. striatum*. A limited number of larvae available, in these larvae the form and size of urogomphi seem to be good characters separating *tenuicorne* from both *striatum* and particularly *punctulatum* (Fig. 32G). Pigmentation usually more brown, with less orange in it.

Host plant: *Pinus*. Habits probably similar to *A. striatum*.

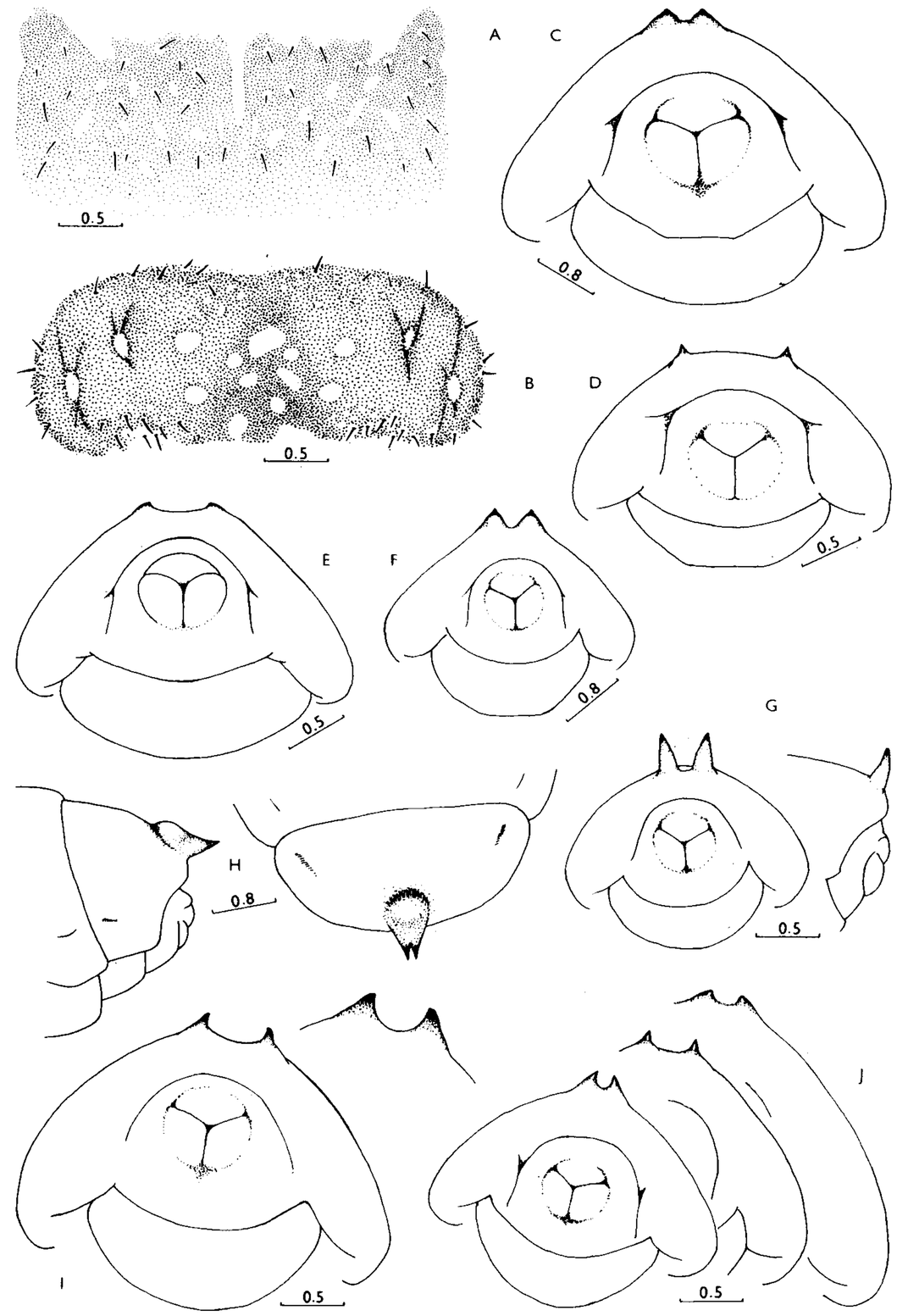
Distribution: Very curious. Crimea, Caucasus, Transcaucasia, Turkey, Syria, Greece, and Gotska Sandön in Sweden! In my opinion it is necessary to carefully examine if we deal with the same species. Also other distribution is not clear, as the species has been apparently occasionally confused with *A. striatum*.

Material: July - August 1970 SU, Krasnodar region, Ubinskaya, 5/I, *Pinus,* lgt. D, coll. IS.

Note: Larvae of the North American *Spondylis upiformis* MANNERHEIM, 1843, have been described by GARDINER (1970a). Two of his larvae are available to me (ex coll. Great Lakes Forest Research Centre, Forest Research Laboratory, Sault Ste. Marie, Ontario, Canada), and they strongly differ not only from *Spondylis buprestoides,* but in some characters they escape from the above description of the whole *Asemum*-group. Short differential characteristic follows:

Cranium slightly more depressed than in other species. Anterior frontal half, very broad genal area and most of ventral sclerite heavily sclerotized, dark brown to pitchy. Clypeus with sides shallowly emarginate, labrum transverse, half-circular,

Plate 32: A — *Asemum striatum,* later instar, microspiculate area of pronotum. B — *Arhopalus rusticus,* mature, second dorsal ambulatory ampulla. C to J — end of abdomen with urogomphi: C — *Megasemum quadricostulatum,* posteroventral view. D — *Spondylis buprestoides,* dtto. E — *Asemum punctulatum,* dtto. F — *As. striatum,* dtto. G — *As. tenuicorne,* posteroventral (left) and lateral (right) views. H — *Arhopalus syriacus,* lateral (left) and dorsal (right) views. I — *Arh. tristis,* posteroventral view. J — *Arh. rusticus,* dtto. (The figure, although drawn from specimens of varying size, shows individual and not growth variability.)



anterior unsclerotized half densely setose. Ventral sclerite short (3.9 in one measured specimen), metatentorial pits rather distant from hind margin. Mandibular type I (!), with sharp simple cutting edge, type II-keel and striated plates fully absent. Mentum with basal pigmented band angulate, pulled forward in middle. Ligula setose, without microtrichial areas of *S. buprestoides,* rather broad, labial palps separated by more than twice their own width. Marginal chambers very few, usually two. Urogomphi small, blunt, subcontiguous, sitting on low common protuberance. Natural length of two available larvae about 20–24 mm.

Judging from the paper by GARDINER (l. c.), the habits are similar to those of *Spondylis buprestoides*. Larvae found in roots of stumps of *Picea glauca*.

Material: 10. 8. 1968 Canada, Alberta, Seebe, 2/I, *Picea,* coll. Forest Insect Disease Survey, Great Lakes For. Res. Centre, Sault Ste. Marie, Ontario, Canada.

In the present generic key the larvae would run more readily to *Tetropium* from which they can be separated by prothoracic epipleurum and lateropraesternum nearly lacking microscopic spines.

REFERENCES

AURIVILLIUS, C., 1912: Cerambycidae: Cerambycinae. Coleopterorum Catalogus Junk - Schenkling, 39. W. Junk, Berlin, 574 pp.

BECKER, G., 1938: Zur Ernährungsphysiologie der Hausbockkäfer-Larven. *Naturwissenschaften* 26: 462–463.

BEESON, C. F. C., 1919: Notes on the larvae and life histories of Prioninae beetles (Col., Cer., Prioninae). *Indian Forest Rec.* 7 (5): 97–119.

BENHAM, G. S., Jr., 1971: Microorganisms associated with immature Prionus laticollis (Col., Cer.). *J. invert. Pathol.* 18: 89–93.

BERRY, R. W., 1972: A rearing procedure for the house longhorn beetle, Hylotrupes bajulus L. (Col.). *Int. Biodeterior. Bull.* 8 (4): 141–144.

BITSCH, J., 1966: L'évolution des structures céphaliques chez les larves de Coléopteres. *Ann. Soc. ent. France* (N. S.) 11: 255–324.

BLACKWELDER, R. E., 1946: Checklist of the coleopterous insects of Mexico, Central America, the West Indies, and South America. Part 4. *Bull. U. S. nat. Mus.* No. 185, Cerambycidae pp. 551–627.

BÖVING, A. G., F. C. CRAIGHEAD, 1931: An illustrated synopsis of the principal larval forms of the order Coleoptera. *Ent. amer.* 11 (N. S.): 1–351.

CAMERON, W. S., P. REAL, 1974: Contribucion a la biologia del coleoptero de la luma, Cheloderus childreni Gray (Col., Cer.). *Rev. chil. Ent.* 8: 123–132.

CANNON, K. F., W. H. ROBINSON, 1982: An artificial diet for the laboratory rearing of the old house borer, Hylotrupes bajulus (Col., Cer.). *Can. Ent.* 114 (8): 739–742.

CERDA, G. M., 1972: Revisión de la subfamilia Oxypeltinae (Col., Cer.). *Publicación ocas. Mus. nac. Hist. nat.* (Santiago de Chile) No. 13: 1–10.

CHARARAS, C., 1979: Écophysiologie des insectes parasites des forets. ?By the author, ?Paris.

CHARARAS, C., 1981: Origine et spécificité des certaines cellulases et hémicellulases chez divers insectes xylophages. *C. R. Acad. Sci.* (Paris) Ser. III, t. 293: 211–214.

CHARARAS, C., J.-M. CHIPOULET, 1983: Studies on the digestion of cellulose by the larvae of the Eucalyptus borer, Phoracantha semipunctata (Col., Cer.). *Austr. J. biol. Sci.* 36: 223–233.

CHARARAS, C., et al., 1983a: Purification of three cellulases from the xylophagous larvae of Ergates faber (Col., Cer.). *Insect Biochem.* 13(2): 213–218.

CHARARAS, C., et al., 1983b: Glycosidases and B group vitamins produced by six yeast strains from the digestive tract of Phoracantha semipunctata larvae and their role in the insect development. *Mycopathologia* 83: 9–15.

CHEREPANOV, A. I., 1979, 81, 82, 83, 84, 85: Usachi severnoi Azii [Longhorn beetles of North Asia] I.–VI. Nauka, Novosibirsk, 472 + 216 + 259 + 222 + 214 + 256 pp.

CRAIGHEAD, F. C., 1915: Larvae of the Prioninae. *U. S. Dept. Agric., Office of the Secretary, Rept.* 107: 1–24, pls. I–VIII.

CRAIGHEAD, F. C., 1916: The determination of the abdominal and thoracic area of the cerambycid larvae as based on the study of the muscles. *Proc. ent. Soc. Wash.* 18 (3): 129–146.

CRAIGHEAD, F. C., 1923: North American cerambycid larvae. *Dom. Canada Dept. Agric. Bull.* No. 27 - N. S. (Technical): 1–239.

CRAIGHEAD, F. C., 1950: Insect enemies of eastern forests. *U. S. Dept. Agric., Misc. Publ.* No. 657: 1–679.

CRAWSHAY, G. A., 1907: The life history of Tetropium gabrieli Ws. *Trans. ent. Soc. Lond.* 1907: 183–212, pls. XV–XX.

CROWSON, R. A., 1981: The Biology of the Coleoptera. Academic Press, New York, XII + 802 pp.

DANILEVSKY, M. L., 1979a: Morfo-adaptivnye puti evolyucii lichinok zhukov-drovosekov (Col., Cer.) i filogeneticheskie svyazi osnovnykh grupp semeistva [Morpho-adaptive ways of evolution of the larvae of longhorn beetles and phylogenetic relations of the basical groups of the family]. In: Nasekomye - razrushiteli drevesiny i ikh entomofagi. Nauka, Moscow, pp. 24–43.

DANILEVSKY, M. L., 1979b: Descriptions of the female, pupa and larva of Apatophysis pavlovskii Plav. and discussion of systematic position of the genus Apatophysis Chevr. (Col., Cer.). *Ent. Obozr.* 58(4): 821–828. (In Russian, English summary.)

DEMELT, C., 1966: Bockkäfer oder Cerambycidae. I. Biologie mitteleuropäischer Bockkäfer (Col., Cer.) unter besonderer Berücksichtigung der Larven. Die Tierwelt Deutschlands, 52. Gustav Fischer Verl., Jena, 115 pp.

DEMELT, C., 1974: Zusammenfassung und Revision der Cerambycidenfauna der Canarischen Inseln. *Nouv. Rev. Ent.* 4(4): 227–235.

DIAS, M. M., 1984: Revisao da subfamília Anoplodermatinae. Parte I. Tribo Anoplodermatini. Genero Migdolus Westwood, 1863 (Col., Cer.). *Rev. bras. Ent.* 28(4): 507–535.

DUFFY, E. A. J., 1946: A contribution towards the biology of Prionus coriarius L. (Col., Cer.). *Trans. roy. ent. Soc. Lond.* 97: 419–442.

DUFFY, E. A. J., 1952: Dorsal prolegs and extreme cephalic modification in the first-instar larva of Agapanthia villosoviridescens Deg. (Col., Cer.). *Ent. mon. Mag.* 87: 313–318.

DUFFY, E. A. J., 1953: A monograph of the immature stages of British and imported timber beetles (Cer.). British Museum (Natural History), London, 350 pp., 8 pls.

DUFFY, E. A. J., 1957: A monograph of the immature stages of African timber beetles (Cer.). British Museum (Natural History), London, 338 pp., 10 pls.

DUFFY, E. A. J., 1960: A monograph of the immature stages of Neotropical timber beetles (Cer.). British Museum (Natural History), London, 327 pp., 13 pls.

DUFFY, E. A. J., 1963: A monograph of the immature stages of Australasian timber beetles (Cer.). British Museum (Natural History), London, 235 pp., 11 pls.

DUFFY, E. A. J., 1968: A monograph of the immature stages of Oriental timber beetles (Cer.). British Museum (Natural History), London, 434 pp., 18 pls.

DUFFY, E. A. J., 1980: A monograph of the immature stages of African timber beetles (Cer.). Supplement. Commonwealth Agricultural Bureaux, Slough, 186 pp., 4 pls.

DUMBLETON, L. J., 1957: The immature stages of some New Zealand longhorn beetles (Col., Cer.). *Trans. roy. Soc. N. Z.* 84: 611–628.

EMDEN, F. I., 1939–40: Larvae of British beetles. 1. A key to the genera and most of the species of British Cerambycid larvae. *Ent. mon. Mag.* 75: 257–273, 76: 7–13.

FONSECA, J. P., 1959: Migdolus morretesi Lane (Coleóptero Anoplodermidae) uma bróca eventual da cana de acúcar e do eucalipto. *Arq. Inst. biol.* (Sao Paulo) 25 (1958): 29–40, 4 pls.

FORCELLA, F., 1982: Why twig-girdling beetles girdle twigs. *Naturwissenschaften* 69(8): 398–400.

FRAGOSO, S. A., 1980: Diaphanous preparations from dark, opaque Coleopterans. *Col. Bull.* 34(2): 143–144.

GARDINER, L. M., 1966: Egg bursters and hatching in the Cerambycidae (Col.). *Can. J. Zool.* 44: 199–212.

GARDINER, L. M., 1970a: Immature stages and habits of Spondylis upiformis Mannerheim (Col., Cer.). *Pan-Pac. Ent.* 46(1): 33–36.

GARDINER, L. M., 1970b: Rearing wood-boring beetles (Cer.) on artificial diet. *Can. Ent.* 102(1): 113–117.

GARDNER, J. C. M., 1931: Immature stages of Indian Coleoptera (8). *Indian Forest Rec.* (*Ent.*) 16(3): 162–202 (correctly 49–89), pls. I–III.

GARDNER, J. C. M., 1942: On larvae of Cerambycidae (Col.). *Indian J. Ent.* 4(2): 103–110.

GRESSIT, J. L., 1951: Longicorn beetles of China. *Longicornia* (Paris) 2: 1–667, 22 pls.

HADLINGTON, P. W., J. A. JOHNSTON, 1974: Mass rearing of Plagiohammus spinipennis (Thoms.) (Col., Cer.) for the biological control of Lantana camara L. (Verbenaceae). *J. ent. Soc. Austral.* (NSW) 8: 32–36.

HATCHETT, J. H., R. D. JACKSON, R. M. BARRY, 1973: Rearing a weed Cerambycid, Dectes texanus, on an artificial medium, with notes on biology (Col.). *Ann. ent. Soc. Am.* 66(3): 519–522.
HAYASHI, M., 1979: Family Cerambycidae (Disteniinae, Parandrinae, Prioninae, Spondylinae, Aseminae). *Checklist Coleopt. Japan* No. 16: 1–6.
HAYASHI, M., K. MORIMOTO, S. KIMOTO, 1984: The Coleoptera of Japan in color, vol. IV. Hoikusha Publ. Co., Osaka, VII + 438 pp. (Cerambycidae pp. 1–146. (In Japanese.)
HESS, W. N., 1917: The chordotonal organs and pleural discs of Cerambycid larvae. *Ann. ent. Soc. Am.* 10(1): 63–74, 4 pls.
HEYROVSKÝ, L., 1955: Fauna ČSR, 5, Cerambycidae. ČSAV Praha, 348 pp.
HORION, A., 1974: Faunistik der mitteleuropäischen Käfer. 12. Cerambycidae - Bockkäfer. By the author, Überlingen-Bodensee, 228 pp.
HOSKING, G. P., 1970: Arhopalus ferus, an introduced Cerambycid borer. *Res. Leafl., Forest Res. Inst.* (Rotorua), No. 29: 1–4.
IMMS, A. D., 1939: A »safe« fluid for museum use. *Nature* (London) 144: 599–600.
KEMMER, N. A., 1918: Über die Gattung Nothorhina Redt. (Col.). *Ent. Tidskr.* 39: 322–328.
KOJIMA, K., M. HAYASHI, 1969: Longicorn beetles. Insects' life in Japan, I. Hoikusha Publ. Co., Osaka, 302 pp. (In Japanese.)
KOJIMA, K., S. NAKAMURA, K. HAMADA, 1966: Morphological notes on nine species of Cerambycid larvae. *Misc. Rep. Hiwa Mus. nat. Hist.* No. 9: 18–24, pls. II–IV. (In Japanese, English summary.)
KOJIMA, T., 1929: Immature stages of some Japanese Cerambycid beetles, with notes on their habits. *J. Coll. Agric. imp. Univ. Tokyo* 10(2): 101–128, pl. VI.
KOJIMA, T., 1931: Further investigation on the immature stages of some Japanese Cerambycid beetles, with notes on their habits. *Ibid.* 11(3): 263–308, pl. XVII.
KUKOR, J. J., M. M. MARTIN, 1983: Acquisition of digestive enzymes by Siricid wood-wasps from their fungal symbiont. *Science* (Washington) 220 (No. 4602): 1161–1163.
KUSAMA, K., M. HAYASHI, 1972: Generic names and type species applied to Japanese Cerambycidae Col.). *Rep. Fac. Sci. Shizuoka Univ.* 6: 95–126.
LAMEERE, A., 1913: Cerambycidae: Prioninae. Coleopterorum Catalogus Junk - Schenkling, 52. W. Junk, Berlin, 108 pp.
LAWRENCE, J. F., A. J. NEWTON JR., 1982: Evolution and classification of beetles. *Annu. Rev. Ecol. Syst.* 13: 261–290.
LEECH, H. B., 1966: Descriptions of the larva and pupa of Necydalis cavipennis LeConte and the pupa of Ortholeptura insignis (Fall) (Col., Cer.). *Occas. Pap. Calif. Acad. Sci.* No. 57: 1–13.
LINSLEY, E. G., 1959: Ecology of Cerambycidae. *Annu Rev. Ent.* 4: 99–138.
LINSLEY, E. G., 1961: The Cerambycidae of North America. Part I: Introduction. *Univ. Calif. Publ. Ent.* No. 18: 1–97, 35 pls.
LINSLEY, E. G., 1962a: The Cerambycidae of North America. Part II: Taxonomy and classification of the Parandrinae, Prioninae, Spondylinae and Aseminae. *Ibid.*, No. 19: 1–103, 1 pl.
LINSLEY, E. G., 1962b: The Cerambycidae of North America. Part III: Taxonomy and classification of the subfamily Cerambycidae, tribes Opsimini through Megaderini. *Ibid.*, No. 20: 1–188.
LYUBARSKY, L. V., 1953: K biologii i ékologii drovoseka-giganta Callipogon (Eoxenus) relictus Sem. (Col., Cer.) [On biology and ecology of Callipogon (Eoxenus) relictus Sem.]. *Ent. Obozr.* 33: 95–102.
LOBANOV, A. L., M. L. DANILEVSKY, S. V. MURZIN, 1981, 1982: Systematic list of longicorn beetles (Col., Cer.) of the USSR. I, II. *Ent. Obozr.* 60(4): 784–803, 61(2): 252–277. (In Russian, English summary.)
MAMAEV, B. M., M. L. DANILEVSKY, 1973: New data on systematic status of the subfamily Aseminae (Col., Cer.), with reference to the morphology of larvae. *Zool. Zh.* 52(8): 1257–1261. (In Russian, English summary.)
MAMAEV, B. M., M. L. DANILEVSKY, 1975: Lichinki zhukov-drovosekov [Larvae of longhorn beetles]. Nauka, Moscow, 282 pp.
MARTIN, M. M., 1984: The role of ingested enzymes in the digestive processes of insects. In: Anderson, J. M., Rayner, A. D. M., Walton, D. W. H. (eds.): Invertebrate-microbial interactions. Cambridge Univ. Press, New York, pp. 155–172.
MISHRA, S. C., P. K. SEN-SHARMA, R. SINGH, 1985: Chemical changes in wood during the digestive process in larvae of Hoplocerambyx spinicornis (Newm.) (Insecta, Col., Cer.). *Mater. Org.* 20(1): 53–64.
MROCZKOWSKI, M., 1986: Tetropium Kirby, 1837 (Insecta, Col., Cer.): Proposed conservation by the suppression of Isarthron Dejean, 1835. *Bull. zool. Nom.* 43(2): 188–190.
NAKAMURA, S., 1981: Morphological and taxonomic studies of Cerambycid pupae in Japan. *Misc. Rep. Hiwa Mus. nat. Hist.* No. 20: 1–159, 75 pls.

OLMI, M., 1975: Nemici della vite. Eccezionali danni provocati in Piemonte dal Coleottero Cerambicide Vesperus strepens F. *Italia Agric.* (Roma) 112(9): 106–111.
PALM, T., 1951: Die Holz- und Rindenkäfer der nordschwedischen Laubbaume. *Meddn Stats. Skogs-Forsk-Inst.* (Stockholm) 40(2): 1–239.
PALM, T., 1956: Zur Kenntnis der Biologie von Acmaeops pratensis Laich. und der verwandten Arten. *Opusc. Ent.* 21: 233–245.
PALM, T., 1957a: Studies über Acmaeops septentrionis C. Thoms. *Ibid.*, 22: 184–188.
PALM, T., 1957b: Zur Kenntnis der Biologie und Ökologie von Pachyta lamed L. *Ent. Tidskr.* 78: 135–142.
PALM, T., 1960: Biologiska studier över Stenocorus meridianus L. (Col., Cer.). *Opusc. Ent.* 25: 138–145.
PALM, T., S. LUNDBERG, 1959: Studier över Acmaeops marginata Fabr. (Col., Cer.). *Ibid.*, 24: 185–191.
PATRICK, C. R., 1973: Observations on the biology of Dectes texanus texanus (Col., Cer.) in Tennessee. *J. Ga. ent. Soc.* 8(4): 277–279.
PAULIAN, R., A. VILLIERS, 1941: Les larves des Cerambycidae français. *Rev. franç. Ent.* 8(4): 202–217.
PAYNE, J. A., H. LOWMAN, R. R. PATE, 1975: Artificial diets for rearing the tilehorned Prionus (Col., Cer.). *Ann. ent. Soc. Am.* 68(4): 680–682.
PLAVILSHCHIKOV, N. N. 1932: Zhuki-drovoseki - vrediteli drevesiny [Longhorn beetles injuring wood]. Goslestekhizdat, Moscow, 200 pp.
PLAVILSHCHIKOV, N. N., 1936: Cerambycidae. 1. Fauna USSR (N. S. No. 7), Insecta, Coleoptera, vol. XXI. Acad. Sci. USSR, Moscow - Leningrad, 611 pp. (In Russian, keys translated into German.)
PLAVILSHCHIKOV, N. N., 1940: Cerambycidae. 2. Fauna USSR (N. S. No. 22), Insecta, Coleoptera, vol. XXII. Acad. Sci. USSR, Moscow - Leningrad, 784 pp. (In Russian, keys translated into German.)
SALIBA, L., 1972: Gallery orientation in Cerambycid larvae. *Entomologist* 105 (No. 1314): 300–304.
SALIBA, L., 1977: Observations on the biology of Cerambyx dux Faldermann in the Maltese Islands (Col., Cer.). *Bull. ent. Res.* 67(1): 107–117.
SAMA, G., 1979: Schurmannia sicula n. gen. et n. sp. di Cerambycidae di Sicilia. *Boll. Mus. civ. Stor. nat.* (Verona) 5 (1978): 369–379.
SAMA, G., P. SCHURMANN, 1980: Coleotteri Cerambicidi di Sicilia. *Animalia* 7: 189–230.
SCOTT, D. A., R. Y. ZACHARUK, 1971: Fine structure of the antennal sensory appendix in the larva of Ctenicera destructor (Brown) (Elateridae, Col.). *Can. J. Zool.* 49: 199–210.
SILFVERBERG, H., 1978: The coleopteran genera of Müller, 1764. *Notul. ent.* 58(3): 117–119.
SILFVERBERG, H., O. BISTRÖM, 1981: Kartering av Finlands langhorningar (Col., Cer.). *Notul. ent.* 61(1): 15–28.
STARZYK, J. R., 1977: Morphology, biology and life history of Carilia (=Neogaurotes Pod.) virginea (L.) (Col., Cer.). *Z. angew. Ent.* 83(3): 269–281.
TEPPNER, H., 1969: Bestimmungstabelle mitteleuropäischer Lamiinae-larven (Col., Cer.), mit Bemerkungen zu deren Biologie. *Verh. zool.-bot. Ges. Wien* 108–109 (1968–69): 19–58.
VILLIERS, A., 1974: Une nouvelle nomenclature des Lepturines de France (Col., Cer.). *Entomologiste* 30(6): 207–217.
VILLIERS, A., 1978: Cerambycidae. Faune des coléoptères de France I (Encyclopédie entomologique XLII). P. Lechevalier, Paris, 636 pp.
WINKLER, A., 1929: Catalogus Coleopterorum regionis palaearcticae. Part X. By the author, Wien. Cerambycidae pp. 1135–1226.

LIST OF TAXA DESCRIBED IN PART I

Non-Palaearctic taxa marked with »+«. Species in square brackets are not formally described, but served as a base for their genera being briefly characterized or keyed. Numbers in round brackets indicate pages with descriptions of the taxa.

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Errata for Part I: Page 9 - delete line 20; p.3 line 15, p.15 line 4, p. 173 line 4 from below - read Gressitt instead of Gressit; p. 38 end of Distenia - read Gardner, 1930 instead of 1930a; p. 57 - line 15 should begin as a new paragraph; p. 174 line 15 - - read Kemner instead of Kemmer; p. 14 line 6 from below - read lacks instead of lack; p. 68 line 6 from below - read constitutes instead of constitute; p. 69 line 20 - read Cerambyx instead of Cerembyx; p. 68 line 9 - read unusual instead of unique; p. 174 line 31 - read A. F. Newton instead of A. J. Newton.
Caution: It now seems possible that the larva determined as Vandykea tuberculata (on which the placement of the genus Vandykea in the subfamily Aseminae has been based) was misidentified. A more detailed commentary on the problem will be found in some of the following volumes.

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