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Saproxylic invertebrates and their conservation

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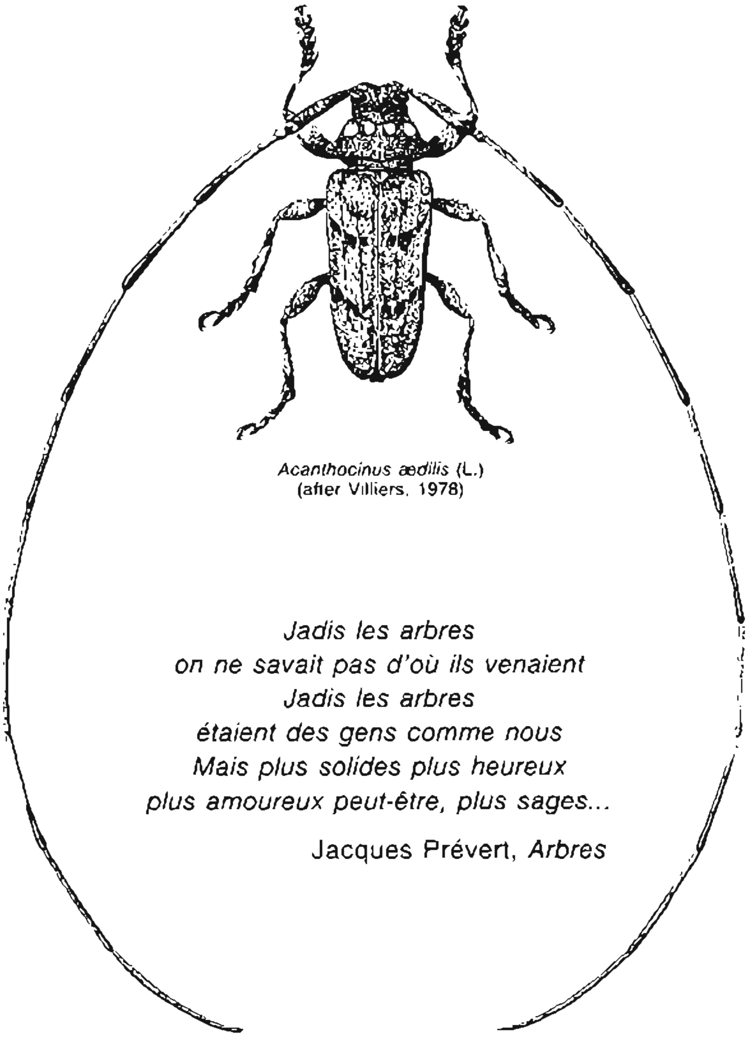
Saproxylic invertebrates and their conservation

Martin C.D. Speight

To the memory of Stefan Plank, who loved old forests and whose statesmanship and dedication contributed much to the success of Council of Europe activities in the sphere of nature conservation



Acanthocinus aedilis (L.)
(after Villiers, 1978)

Jadis les arbres
on ne savait pas d'où ils venaient
Jadis les arbres
étaient des gens comme nous
Mais plus solides plus heureux
plus amoureux peut-être, plus sages...

Jacques Prévert, *Arbres*

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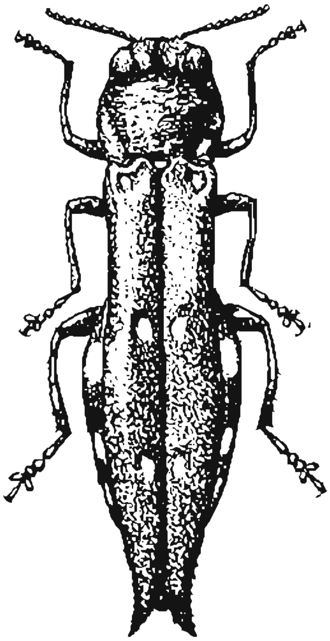


<u>Agrilus</u> <u>guerini</u>,
A buprestid beetle
/ un bupreste
(after / après
Liskenne, 1986)

1. INTRODUCTION

1.1. Saproxylic Invertebrates: a definition

Species of invertebrate that are dependent, during some part of their life cycle, upon the dead or dying wood of moribund or dead trees (standing or fallen), or upon wood-inhabiting fungi, or upon the presence of other saproxylics.

1.2. The Saproxylic Invertebrates Project

In 1980, the Council of Europe set up a Consultants' Group to identify projects related to invertebrate conservation which might be incorporated into the work programme of the then CDSN committee. A particular objective was to identify projects which would be able to take advantage of the invertebrates' potential as bio-indicators. One of the projects defined by that consultants' group and later adopted into the work programme was the "Saproxylic Invertebrates" project. Using selected saproxylic insects as bio-indicators of site quality to compile a list of high-quality forests, this project was envisaged as having the dual objectives of:

a) aiding in the process of identifying forests of international importance for nature conservation,

b) aiding in the conservation of a diverse and seriously threatened assemblage of invertebrates important in the recycling of energy and nutrients in natural forest

In recommending this project, the consultants took into consideration the fact that while projects based on flowering plants gave indications of the state of health of primary production in ecosystems, and vertebrate-based projects similarly provided data about secondary production, in order to gain some insight into the decomposer sector, responsible for recycling of nutrients through the biosphere, it was necessary to deal with invertebrates, fungi or micro-organisms. Forests, with their production of great quantities of woody tissue, are recognised as manifesting the most complex decomposer communities found among terrestrial ecosystems. Given that, at this point in time, projects based on fungi or micro-organisms are less likely to meet with success due to difficulties of gathering the necessary data, a project based on saproxylic invertebrates as bio-indicators could be seen to be an appropriate choice.

During discussion of the project, concern was expressed that invertebrates were by and large terra incognita to most people and that, in particular, the part played by saproxylics in natural forest was not generally understood. Similarly, it was felt that there was need for consideration of mechanisms that might be employed for conservation of such organisms, beyond simply setting aside areas of forest for their protection. These issues have been taken into account during production of the present report. To show why saproxylic invertebrates are regarded as under threat in Europe, background data on their current status has been briefly reviewed here, together with a short account of how the present situation has developed. In the hope that it will help to place saproxylics in their natural surroundings, a chapter on the species and their habitats has been included. The role of saproxylic invertebrates is played out during the process of decomposition of wood, and the interplay between the activities of saproxylic invertebrates, saproxylic fungi and micro-organisms is in this process all pervasive. This is acknowledged here, the part played by saproxylic invertebrates being described largely within the context of the story of natural wood decay, along with description of the roles of fungi and bacteria. In the final chapter, attention is given to problems in the conservation of saproxylic invertebrates and ways in which these problems may be overcome, demonstrating in the process how the material presented in the other chapters of the report has a bearing on the actions which can usefully be taken. Although relatively short, this report touches on a number of rather different topics. An extensive set of references has accordingly been included, to aid those who might wish to explore any of these topics more deeply.

1.3. Methodology

The first step taken was to derive a set of criteria for use in selection of the saproxylics to be employed as bio-indicators of site quality. These criteria were set out in document SN-VS (82) 3 and subsequently agreed at a meeting of the consultants' group convened to review progress on the project. It was in this way decided that the species selected for this project should be chosen from among European insects which are:

1. associated with the dominant, long-lived climax tree species of European forests,
2. dependent upon dead wood of senescent and dead trees for their habitats
3. regarded as being today excessively localised in their European distribution
4. of moderate to large size
5. relatively easy to find
6. relatively easy to determine

Using these criteria, a list of 33 saproxylic insect species was compiled. These species are listed below, with the tree genus each is most closely associated with given in brackets:

COLEOPTERA

Buprestidae: Buprestis splendens (Abies); Dicerca acuminata (Betula); D.alni (Alnus); Eurythraea austriaca (Abies); E.quercus (Quercus); Kisanthobia ariasi (Quercus)

Cerambycidae: Akimerus schaefferi (Quercus); Anisorus quercus (Quercus); Brachyleptura strangulata (Pinus); Cornumutila 4-vittata (Larix/Picea); Glaphyra marmottani (Pinus); Hesperophanes pallidus (Quercus/Tilia); Icosium tomentosum (Juniperus); Leptura arcuata (Alnus); Lioderina linearis(Abies); Megopis scabricornis (Quercus etc.); Necydalis ulmi (Fagus/Quercus); Oxypleurus nodieri (Pinus);

Rhopalopus ungaricus (Acer); Tragosoma depsarium (Picea/Pinus)
Cetoniidae: Gnorimus 8-punctatus (Quercus); Liocola lugubris (Quercus); Posotia aeruginosa (Quercus); P.koenigi (Quercus)
Elateridae: Ampedus 4-signatus (Quercus); Lacon lepidopterus (Pinus); L.punctata (Pinus etc.)
Lucanidae: Ceruchus tenebriodes
Rhysodidae: Rhysodes sulcatus

DIPTERA
Asilidae: Laphria ephippium (Fagus); L.gibbosa(Picea)
Keroplatidae: Keroplatus tipuloides (Fagus)
Syrphidae: Caliprobola speciosa (Fagus)

In discussion, the consultants subsequently concluded that use of this list was not likely to produce the desired result, because these species were already so localised within their European range that any forest list based only upon localities where they occurred would be excessively brief and omit forests supporting other, equally relevant species. The decision was therefor taken to considerably expand the species list, resulting in the production of a list incorporating the species indicated in Appendix 1 of the present report. The majority of the listed species have range and distribution characteristics typified by Rhysodes sulcatus (detailed in the following section of this report, on Status of saproxylics), in that they are known today from only a few, widely scattered locations. Others are known from only within a single, very restricted part of Europe. A very few of them, noteably the two ground beetles (Carabidae) listed, are extremely localised over by far the greater part of their European range but not threatened in some limited area. All of the listed species can be regarded as vulnerable to extinction in Europe now. Nearly all of them would fall into the "endangered" category in all parts of their European range. The list in Appendix 1 is not, and is not presented as, a comprehensive list of Europe's threatened saproxylic insects. It is merely a selection, from among the threatened species, of organisms which meet the criteria given above.

Following its production, the extended species list was circulated to interested specialists and organisations suggested by the consultants. The species list was accompanied by a text explaining the project and its objectives and by return forms for recipients to fill in with details of forests they proposed for inclusion in the forest list. Details of the project appeared in the literature of some entomological societies and national biological recording centres. The project was detailed at a meeting of the Europoean Invertebrate Survey Committee (EIS), and thereafter enjoyed the active support of EIS members.

Contributors were asked to provide the following data for each forest:

a) the name of the forest,
b) the location of the forest, including the name of the administrative region in which it was to be found,
c) the generic names of the trees dominant in the forest,

d) details of any published references to the occurrence of saproxylic invertebrates in the forest
e) details of any unpublished data available to them, on the saproxylics occurring in the forest
f) whether or no they wished the unpublished data to remain confidential

From the returns received during this phase of the project a list of forests was compiled which included a majority of those listed in Appendix 2. These results, together with a text relating to the second phase of the project, were then submitted to the Council of Europe Committee of Experts in Conservation of Wildlife and Natural Habitats (SN-VS). When the committee agreed that the second phase of the project should proceed, a text explaining this phase was circulated as before, together with copies of the list of forests compiled during the first phase. This phase was also announced in the EIS Newsletter and at the Third European Congress of Entomology, in Amsterdam.

During the second phase of the project, contributors were asked to forward details of forests considered by them to contain saproxylic faunas probably as diverse as those to be found in the forests already listed, based on any invertebrate data at their disposal. In this way data relating to saproxylics not on the species list could be tapped and potentially important forests from which minimal information was available could be included in the list. The latter group of forests, those included on the basis of minimum information, are asterisked in Appendix 2. The details of publications referred to by contributors, as listing saproxylics recorded from forests included in Appendix 2, are incorporated into the References section of this report.

1.4. The list of forests

Inevitably, it proved easier to obtain data from some parts of Europe than from others. No information at all was obtained from Portugal. There is at least one potentially listable forest in Luxembourg, but data on saproxylics are unavailable for it. No forests appropriate for listing could be found in either Ireland or the Netherlands. Data was contributed for some parts of France, Greece, Italy and Spain, but not for other parts. The good information for some regions is due to considerable assistance from a small number of individuals who did their best to extract data from their colleagues. Some individuals known to possess relevant data have unfortunately failed to respond. In one or two instances, recent legislation prohibiting collection of insects has made it impossible for even the staff of reputable institutions like State Museums to carry out survey work in potentially important forests. This has resulted in a lack of up-to-date information on the faunas of certain forests which have thus been included in the list on the basis of only rather old data.

The listed forests include a majority within mountainous parts of the continent. Lowland and valley forests are noticeably lacking. This is true not only for Western Europe, but central Europe and Scandinavia as well. No lowland forests could be listed for Switzerland, apart from some remnants so small as to be only doubtfully worth including. The same is true for Sweden. Particularly noticeable is the almost total absence from the list of areas of alluvial forest.

The list comprises the names of approximately 150 forests. Some of them are of respectable size, others are of as little as 40 hectares. In the opening paragraphs of the chapter on Conservation, the feasibility of maintaining forest conditions within areas of under 400-500 hectares is questioned. How can remnants of 40 hectares contribute usefully to conservation of saproxylics? Some suggestions are made in this subject area in the chapter on Conservation, but, realistically, the only hope for such small forest enclaves is that they be enlarged by addition and appropriate management of surrounding land. The fact remains, though, that the forests listed in Appendix 2 are by no means all equally viable. In particular, they vary in their potential for providing a continuity of habitats appropriate for saproxylics. The smaller forests among them are likely to lack old trees and dead wood for decades, once the current generation of over-mature specimens dies. Again, in the Conservation chapter, possible ways of overcoming this problem are considered. But the first step, the primary step, towards conservation of Europe's saproxylic flora and fauna, would be to secure the listed forests for protection of wildlife. The list may be incomplete, but if the forests included upon it were set aside for nature conservation this would represent a drammatic improvement over the present circumstance. Until now, the plight of the saproxylics has not been recognised, the significance of their role in natural forest has been ignored, and only a handful of European forests supporting a recognisably diverse saproxylic community has been secured for protection.

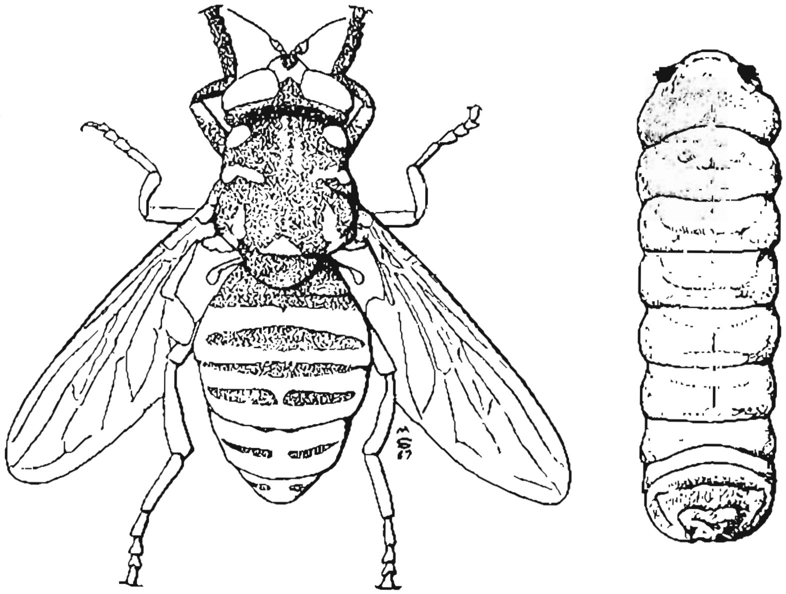


FIG. 1.1.: *Temnostoma vespiforme*, a wasp-mimicking hoverfly with saproxylic larvae (at right). The larvae tunnel firm wood within rotting logs and stumps. Although widely distributed. this insect is now becoming very localised. (larva after Stammer. 1933)

2. THE STATUS OF SAPROXYLIC INVERTEBRATES IN EUROPE

Although less information has been gathered together about invertebrates than other animal groups, it is apparent that they are subject to the same threats as other organisms and that, each time a group of invertebrates is investigated, a suite of species is identified as in danger of extinction in the continent. The most recent study of a group of invertebrates carried out by the Council of Europe, on dragonflies (see van Tol & Verdonk, 1986), demostrates this clearly. There are grounds for asserting that 20% of Europe's terrestrial and freshwater invertebrate species may currently be vulnerable to extinction(Speight, 1984, 1985). Increasing concern for Europe's invertebrate fauna prompted the Council of Europe to adopt, in 1986, the Charter on Invertebrates (see Pavan, 1986). In the following paragraphs brief consideration is given to the extent to which saproxylic invertebrates, as a group, are under threat.

2.1. The post-glacial history of Europe's saproxylic fauna

The Vegetation Map of the Council of Europe member states (Ozenda et al, 1979) shows clearly the extent to which the continent would be covered in forests were it not for man's intervention. The differences between that map and what is found on the ground in the Europe of today are staggering and demonstrate, in particular, that the natural tree cover has been eliminated from all but a residual percentage of its previous area. An inevitable consequence of the loss of the trees is loss of their dependent fauna. Saproxylic invertebrates represent a substantial proportion of the fauna dependent upon trees, and old trees in particular.

2.1.1. The felling of Europe's indigenous forest

A little-appreciated feature of the process of progressive eradication of Europe's saproxylic fauna (and flora) is its great antiquity. By 3000BC man had begun to make significant inroads into the forest area almost throughout the continent. By 2000 years ago it is doubtful that anything more than patches of secondary forest remained in the lowlands, over most of the mediterrannean region (see Smith, 1979)and those parts of western Europe accessible to the primitive ploughs then available (Bell & Limbrey, 1982, Fowler, 1971). By the time Linnaeus started to give plants and animals Latin names, Europe's forest area had been reduced to its smallest extent since the last glaciation; practices of "forest hygiene" had been established which led to removal of moribund and dead trees; wherever it was accessible fallen timber was highly sought after as firewood and saproxylics had already been lost from extensive areas of their postglacial range. As Tubbs (1976) says of the situation in Britain "The destruction of the natural woodland cover between the Neolithic and Tudor times was remarkably complete and left little more than fragments of woodland much modified by long histories of cropping, casual exploitation or grazing."

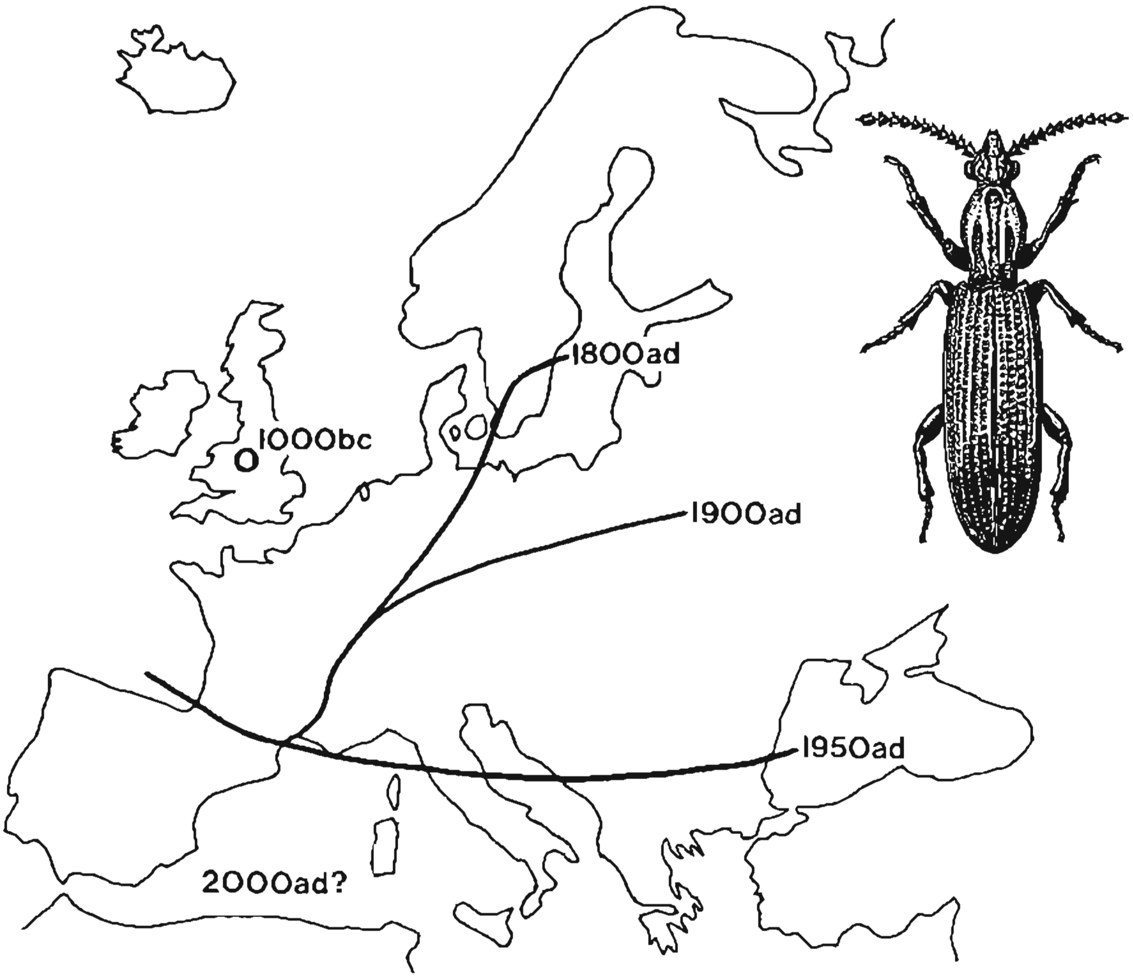


FIG. 2.1: *Rhysodes sulcatus* (Fab.), figured at right (after Dendaletche, 1973) is a saproxylic beetle that is becoming extinct. The map shows, diagrammatically, the progressive contraction of its range, starting some time within the last 3000 years with its disappearance from Great Britain. Today, it is known in the Council of Europe area from only a handful of localities in Southern Europe. It has also been found in the Balkans and Caucasus mountains, but its present status there is unknown. / *R.sulcatus*, figuré à la droite (après Dendaletche, 1973) est un coléoptère saproxylique en train de disparition. La carte suggere, en forme diagramatique, sa diminution, commençant avec son éclipse en Grande Bretagne pendant les derniers 3000 d'ans. A l'heure actuelle, il est connu seulement de quelques points dans les Pyrenées et les montagnes d'Italie et en Grèce. On ne sait pas s'il existe encore dans les Balkans ou Le Caucase.

2.1.2. Extinctions in pre-Linnaean Europe

Despite the small amount of work which has been carried out on the remains of invertebrates preserved in post-glacial deposits, Girling(1982) was able to list 20 saproxylic beetle species which had occurred in bronze-age Britain, but which had disappeared prior to Linnaeus. A diagrammatic representation of the postglacial history of one of these insects, Rhysodes sulcatus, is shown in fig. 2.1. From the present-day European distribution of this beetle the fact that it once ranged throughout Europe would be almost impossible to deduce. From what is known of the species listed in Appendix 1, all too many of them exhibit disjunct distribution patterns in Europe, like that of R.sulcatus. The inadequacy of our information makes extrapolation perilous, but the existing data do show that R.sulcatus is not alone in exhibiting a drammatic decrease in its European range between the neolithic period and the beginning of the period of major re-afforestation which got underway in the 18th. century. For the saproxylic invertebrates then, there are indications that a major phase of extinction took place in Europe prior to the onset of the scientific period, that left these organisms localised in scattered enclaves of more or less natural forest. These remnants of natural forest have continued to dwindle in number up to the present day. This process of gradual attrition has largely gone unrecorded, but there are the occasional forlorn accounts of individual forests, such as that of MacDermot (1973), which opens with the words "This book is an attempt at a continuous history of Exmoor Forest from the earliest times, down to the extinction of the forest in 1819".

In parts of the intensively used lowland regions of the mediterranean basin, or Western Europe, or offshore islands such as Great Britain and Ireland, it is not beyond the bounds of possibility that the major part of the local saproxylic fauna was eradicated by forest clearance before entomologists and others began to compile faunal lists. Indeed, it is difficult to explain the peculiarly limited saproxylic faunas recorded from forests in some of these regions in any other way. Ireland represents an extreme case of this phenomenon, lacking a total of 600 of the woodland beetle species recorded in Great Britain (Hammond, 1974), nearly all of which can occur on trees indigenous to Ireland. Taking the cerambycid beetles as an example, of those species attached to trees indigenous to Ireland, six times as many are recorded in N.France as in Ireland. Britain is in an intermediate position, with half of the species found in N.France. Cerambycids are highly mobile and tend to predominate in island faunas difficult for less mobile insects to reach, so there is no justification for arguing that cerambycids are under-represented in Great Britain and Ireland because they were unable to reach those islands.

2.1.3. Replacement of forest by conifer plantation

The replanting and re-afforestation process which has occurred in Europe latterly has been of little benefit to saproxylics. On the one hand the new forests are mostly of non-native conifers introduced to parts of Europe where the indigenous saproxylics are dependent upon the wood of broad-leaved trees, and on the other, the moribund and dead trees which provide the required habitats for saproxylics are conscientiously removed from these new forests as soon as they appear, due to the dictates of commercial forestry practise. Disquiet at the general ecological consequences of this coniferisation process gave rise to the first publication in the Council of Europe's Nature and Environment Series (Noirfalise, 1968). Present-day forestry activities can be shown to have a detrimental effect upon most wildlife (Peterken & Harding, 1975) but, as Heliovaara & Vaisanen (1984) conclude, when considering the 80% drop in faunal species diversity that has been estimated to accompany conversion of natural forest to commercial tree plantation, it is the organisms associated with the over-mature trees and dead wood of indigenous European forest types which have suffered most from forestry activities. Their dependence upon habitats absent from the burgeoning mass of conifer plantations that has come to occupy Europe's erstwhile forested regions in the last two centuries has done nothing to check the descent of saproxylics toward oblivion, but much to hasten their demise. The saproxylics dependent upon the wood of deciduous trees have been drastically affected, leaving many of them verging on extinction, as can be seen from National Lists of threatened species. Sadly, as the eloquent words of Rabil(1977) record, this "coniferisation" process is still, today, eradicating areas of ancient deciduous forest. The sort of ministerial policy statement he quotes, that "la forêt doit être gerée comme un champ de petits pois ou de tomates", encapsulates an attitude frequent within forestry organisations over much of the continent.

2.1.4. Extinctions during the 18th. and early 19th. centuries

Along with certain wetland species, a number of saproxylics are among the first invertebrates recorded as becoming extinct in parts of post-Linnaean Europe. For example, by 1800 Cerophytum elateroides had disappeared from Britain and Buprestis splendens and Rhysodes sulcatus had gone from Scandinavia, though specimens of these species exist, collected from these parts of Europe before this date. In total, nearly 20 saproxylic beetle species are believed to have become extinct in Great Britain during this period (Shirt, 1987). Needless to say, there are comparatively few insect specimens which have survived in collections since this early time, and of the existing specimens many are of doubtful provenance. The fact that it is possible to demonstrate at all that saproxylic species were disappearing during the eighteenth century implies that, were our data more complete, a staggering amount of range contraction among saproxylics would be revealed, for the eighteenth and early nineteenth centuries. It should be noted that among the "doubtful" early records are a number for saproxylic species and that one of the reasons for the reluctance of authors to accept these records appears to be an assumption that organisms like insects did not become extinct during this period. To quote but one example, writing on one of Europe's most unmistakeable hoverflies (Syrphidae), the saproxylic Temnostoma vespiforme (fig. 1.1) , which on supposedly reliable authority had been recorded in Britain at the beginning of the nineteenth century but not subsequently, Verrall(1901) said "I do not think that so conspicuous an insect would have been overlooked ever since" and excluded the species from his British list. Later authors have not questioned Verrall's logic and T.vespiforme has not appeared on British species lists since Verrall's work was published. Without question, this type of treatment of early records has led to a reduction in the extent to which the question of eighteenth and early nineteenth century extinctions of saproxylics has been given serious consideration and consequent under-estimation of the scale of the phenomenon. Early records of Cerambyx cerdo and Strangalia attenuata from Britian were given the same treatment as those for T.vespiforme, until indisputable evidence for the presence of these beetles was obtained from the British neolithic period (Girling, 1982, 1984).

2.1.5. Present-day isolation of populations of saproxylics

Knowledge of the age and history of individual forests in Europe is not very complete, except for those established within the last two or three hundred years and such information can be difficult to come by even for forests believed to be of quite recent origin. Nonetheless, a noticeable feature of the forests listed in Appendix 2 is that they tend to be of great antiquity. In Western Europe, in particular, few are as recently established as the Foret de Loches, believed to have been established some 500 years ago. The British forests listed represent an extreme, all believed to have been in situ for a thousand years or more. Forests known to have been established within the last 200-300 years, even if they do today contain trees of 200-300 years old, hardly figure in the list at all. This would imply that the sites which do retain a highly differentiated fauna of saproxylic invertebrates are not acting as sources from which saproxylics can disperse into new areas of appropriate habitat. The most plausible explanation for such a situation would be that the ancient forests with a rich fauna of saproxylics are now so few and far between and so distant from other, more recent, forests which might provide appropriate habitats for saproxylics, that colonisation of these recent forests is not possible. This would mean that, zoogeographically, the forests which today could support highly differentiated saproxylic faunas have effectively become islands, within a sea of hostile terrain too vast for saproxylics to successfully traverse. It is also likely that effective establishment of saproxylics is prevented by the small size of remaining enclaves of appropriate forest. As Stevens (1986) has observed, a host-tree available in only small quantity generally accumulates only a few of its dependent saproxylics.

2.2. The state of knowledge in relation to present distribution of individual saproxylic species

Surveys of the distribution of saproxylic invertebrates, sufficiently precise to allow the mapping of individual species throughout Europe, have not, as yet, been carried out. In order to assess the status of species it is thus necessary to make recourse to diverse literature sources and specialists who have knowledge of the saproxylic fauna in their own part of the continent. Use of such data sources tends to result in over-optimistic conclusions concerning the better-known species, due to the tendency to include records from the beginning of the century from sites that have not been visited subsequently but may have by now become uninhabitable by saproxylics. Conversely, using the same data sources, the status of poorly studied species can be over-pessimistically assessed due to the existence of a significant number of unsuspected populations of the species. But it is also true that, in the case of a saproxylic species, whose habitats are virtually nonexistant in farmland or commercial forests, there are now few sites worthy of survey in any effort to establish its precise distribution.

A maximum figure of 10% of the land surface of most European countries remains today in some more or less "semi-natural" condition (Speight, 1986b) and only a minute fraction of that semi-natural area is forested. Few of the forests involved can be expected to be inhabitable by saproxylics. A recent survey in Belgium failed to locate even a single oak old enough to be dying of old age, for example (J.Leclerq, pers.comm.). So, in estimating the status of European saproxylics, mistakes made in assigning species to a particular status category are unlikely to involve classifying many non-threatened species as threatened, because forests which could potentially support saproxylics are themselves in short supply. A majority of the saproxylic invertebrates could probably properly be included in the IUCN "vulnerable" category throughout most of their European range. Few indeed are the saproxylics not now classifiable as vulnerable to extinction in some part of their European range where they were once common. Ireland, once extensively covered in oak and pine forests, provides an extreme example. The indigenous pine (<u>Pinus sylvestris</u>) has disappeared from the Irish landscape and whatever saproxylic fauna it had has quite disappeared with it (Speight, 1985b). Even saproxylics like <u>Pterostichus oblongopunctatus</u>, still widely distributed and not uncommon in deciduous woods in many parts of Europe, are now extremely localised in Ireland (Speight et al, 1983).

Of all the taxonomic groups of invertebrates which contribute species to the saproxylic complex of Europe's forests, the longhorn beetles (Cerambycidae) are arguably the most prominent, in that they are both well known and important in the role they play as primary and secondary saproxylics (see text on the process of wood decomposition). They are also among the most effective colonists of new sites and Villiers (1978) is able to refer to a number of conifer-inhabiting cerambycids which have been able to extent their range recently, using the cut stumps found in commercial conifer plantations. But, regrettably, even in this highly mobile group, known for their ability to establish themselves on oceanic islands, only a minority of species have been able to expand their range in Europe via conifer plantations and none of the species attached to deciduous trees exhibits this expansion. Villiers (loc.cit.) goes on to classify 40% of the saproxylic cerambycids occurring in France as rare. A similar percentage of the Austrian cerambycid fauna is classified as threatened by Gepp (1983). Of the more than 150 saproxylic beetle species listed by Andersson et al (1987) as threatened in Sweden, some 40% are cerambycids. Species dependent upon conifers predominate in the Swedish cerambycid fauna, but even so more than 20% of the cerambycid species of Sweden are regarded as threatened, a proportion only exceeded by other beetle families in which saproxylic species predominate. Given that cerambycids have to be regarded as among the most effective of colonisers among the saproxylics, it is perhaps not surprising to discover that saproxylics in other taxonomic groups are considered to be even more seriously threatened. Gepp (loc.cit.), for instance, suggests that while only 1% of Austrian cerambycids are probably already extinct, more than 10% of the Austrian saproxylic beetle fauna in general would fall into this category. Writing on the aradid bugs, Heliovaarna and Vaisanen (1983) conclude that of the 18 Finnish species 5 are probably extinct, 5 others are now rare or very rare, 7 more are declining and only 1 is increasing. The same species recognised by Heliovaarna and Vaisanen as either extinct or rare in Finland are also listed as under threat in Sweden, by Andersson et al (1987).

With the large number of taxonomic groups involved and the fragmentary nature of the literature, it is difficult to gain an overview of the state of the entire European fauna of saproxylic invertebrates. However, together with data pertaining to the availability of forests which might be able to support saproxylics, the sources consulted during compilation of this text would suggest that some 40% of Europe's saproxylic invertebrates are already threatened over much of their European range and that the majority of the remainder are in decline. Conversely, only some 10% of the European species might be regarded as not in need of some protection.

A vague notion which seems to be very widespread is that, if a nature reserve or other protected area is established, it will be colonised from "somewhere" by invertebrate species worthy of conservation. This impression possibly derives from the fact that invertebrate surveys are rarely carried out before such protected areas are established, so that when they are carried out later and reveal the presence of invertebrate species recognised as requiring protection, it is presumed that these species have only just arrived, rather than that they were probably present throughout. In many parts of Europe, protected forests which do not contain well-differentiated faunas of saproxylic invertebrates are very unlikely to experience a diversification of their saproxylic fauna by spontaneous colonisation from elsewhere, because, as suggested earlier, there are now so few sources of saproxylics available and they are so far between (see for instance, Wormell, 1977). Similarly, protected forests cannot be expected to experience a resurgence of saproxylics because provision of appropriate habitats has triggered an emergence of species from some condition of dormancy or suspended animation. Saproxylic invertebrates possess no convenient mechanism like dormant seeds or spores, by means of which they can survive periods in which their habitats are lacking from a forest. These facts put endangered saproxylic invertebrates into a different situation from some other categories of threatened flora and fauna.

Establishment of a protected area within a forest still possessing a diverse fauna of saproxylics may help to stabilise populations of some endangered saproxylic species, but is unlikely to result in them thereafter being able to spread out through the surrounding countryside. Essentially, the uses made of land by man condemn saproxylics to remaining on lists of threatened species far into the future, and each saproxylic fauna that is lost will not be easy to replace by processes of habitat provision on new sites. This scenario is made grimmer when it is recognised how very localised so many saproxylic invertebrates have already become. Examples have already been given of the decline and fall of a number of species, typified by Rhysodes sulcatus. This beetle now survives in Europe only in a handful of localities in the Pyrenees and mountainous parts of Italy and N.Greece. Perhaps exhaustive search will reveal it does still exist in some forest in central Europe. But even if so, R.sulcatus will remain an extremely threatened species. When one of the few remaiming forests recognised as possessing a rich saproxylic fauna is subject to detailed survey it almost invariably results in discovery of one or two species existing far beyond what was previously thought to be their range, demonstrating the extent to which species have been eradicated from immense tracts of territory. The striking, red and black click-beetle Ampedus quadrisignatus is an example. Thought to be confined to central Europe during the present century, although once extending as far West as the Vosges mountains of E.France (where it was last recorded in 1847), in 1961 this beetle was discovered in the relict beech forest of Massane, in the Pyrennes (Dajoz, 1965), nearly 1000km. from any other extant population.

The large, black and yellow, dramatic-looking fly Solva interrupta, whose larvae live beneath the bark of moribund aspen (Populus tremula), was only discovered in 1926. It has never been found outside Finland and an adjacent strip of the USSR, and has only been found at a total of 9 different localities (Vaisanen, 1982). Another large, wasp-mimicking fly, Doros destillatorius, which inhabits ancient beech forests in Southern Europe, has been found on only five occasions (Speight, in press). Only three Doros species are known in the world. Two of them occur in Europe and both European species are threatened. A very similar situation exists for the relict fly family Canthyloscelidae, one specimen of which was recently captured in Switzerland (Haenni & Dufour, 1983), there being 7 European and two Asian records in all for the two Palaearctic species belonging to the family. The forests of Corsica support a range of saproxylics which have never been found elsewhere. As Crowson (1981) points out, such organisms can only very doubtfully be regarded as true endemics and are much more likely to be relict populations of species much more widely distributed in the past.

3. THE ORGANISMS AND THEIR HABITATS

In Europe, saproxylic invertebrates number many hundreds of species. Derksen(1941) referred to 32 families of Coleoptera alone, as involved in the recycling of timber in a German beech (Fagus) woodland. The longhorn beetles (Cerambycidae) include more than 500 saproxylic, European species. Saproxylics may exhibit a high degree of sophistication in their life styles and a high degree of habitat fidelity. The objective of this section of the text is to provide an overview of how these organisms fit into the physical environments that develop as a tree begins to decay and die.

3.1. Invertebrate habitats

The "habitat" of a brown bear is a rather different phenomenon from the "habitat" of a typical species of saproxylic invertebrate. An individual bear may have a territory embracing a wide range of different biotopes and several thousand metres of altitude. A self-contained population of a wood-boring beetle species may go through many successive generations within one rotten tree. Moreover, any given generation is more likely than not to inhabit only one part of a rotten tree, with other species using different parts of the same tree.

Invertebrates are pre-adapted to exploiting resources which are available in only small quantities. To human perception, a moribund tree may seem to represent one, rather substantial resource. But to organisms involved in recycling the materials comprising a moribund tree, its various components each present very different problems. Bark is chemically very different from heartwood. The physical environmental conditions surrounding a dead branch differ widely from those surrounding a dead root. Interactions between organisms differentiate the materials further - some saproxylic invertebrates feed only on wood already processed by saproxylic fungi, while others live only in burrows left behind by wood-boring species. Yet others are specialist predators or parasites of saproxylic species. To the saproxylic fauna, a moribund, over-mature tree represents not a habitat but a multiplicity of habitats. It is not so much an individual abode as a megalopolis. The inhabitants of this megalopolis include representatives of many different taxonomic groups and (Hamilton(1978) a surprisingly large number of the species are the only known living examples of often quite major groups.

3.2. The arboreal megalopolis

In a mature, healthy tree (fig. 3.1) there may seem to be no place for saproxylics. But, by the time the tree has reached an age of 150 years, some fraction of its woody parts is likely to have been damaged and to have died, and accumulation of tree humus can have started in rot-holes. By this stage then (fig. 3.2)

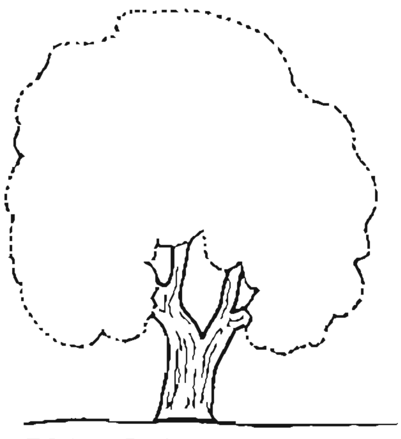


FIG. 3.1

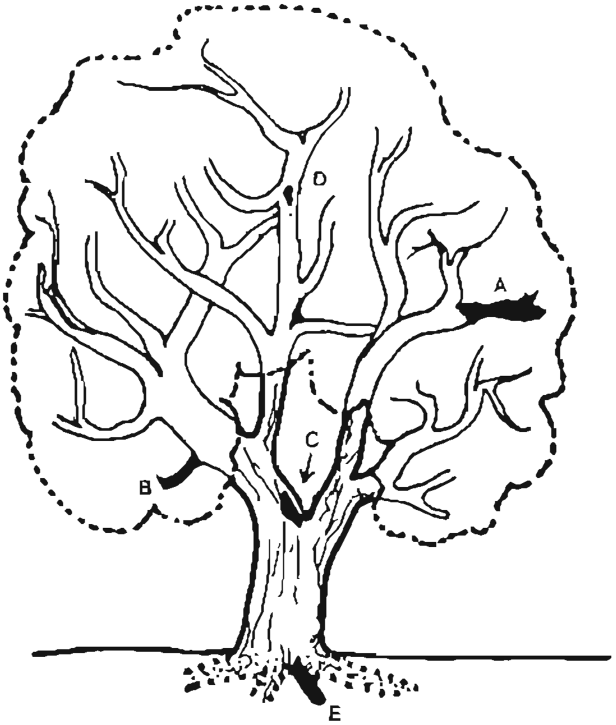


FIG. 3.2: As the tree ages, parts become diseased or damaged, providing habitats which saproxylics can colonise. Such habitats are marked in solid black on the figure / L'âge venant, certains de ses parties s'abîment ou deviennient malades et fournissent ainsi des habitats que les saproxyliques peuvent se mettre à coloniser. Ces habitats sont marqués en noir sur la figure
A, B = dead branches / branches mortes; C, D = rot-holes / trous de carie; E = dead root / racine morte

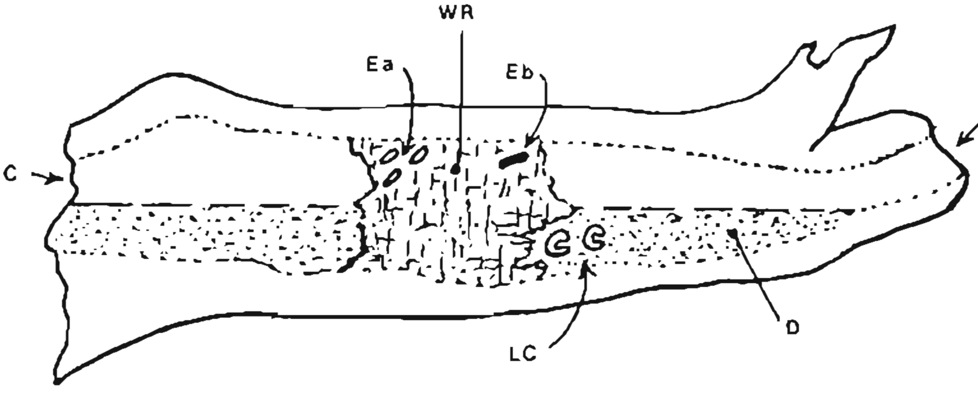


FIG. 3.3.: When the dead branch (A) shown in Fig. 3.2. falls to the ground, much of its substance will have already been decomposed by saproxylics, leaving it partly hollow and with a residue of wood dust lying in the cavity / Lorsque la branche morte (A) repérée sur la Fig. 3.2. tombe à terre, sa substance est déjà fortement décomposée par les espèces saproxyliques qui l'ont en partie évidé et ont laissé dans la cavité de la poussière de bois:
C = cavity / cavité; D = wood dust (produced by passage of wood through alimentary canal of saproxylics) / poussière de bois (produite par le passage du bois par leur tube digestif); Ea, Eb = larvae of different elaterid beetles / larves d'elaterides; LC = larvae of cetoniid beetles / larves de cetoniides; WR = red-coloured, friable dead wood (result of attack by brown-rot fungi) / bois mort, roussâtre et friable (qui a été attaqué par des champignons lignicoles)

a fauna of saproxylics can begin to establish itself in the occasional dead branch(fig. 3.3), dead root or humus hollow.

As time progresses the proportion of damaged and dead timber carried by the tree increases, until by the time it is in excess of 250-300 years old the presence of habitats for saproxylics can be obvious(fig. 3.4), including features like massive, broken limbs, trunk cancers, trunk cavities, fallen branches, etc.

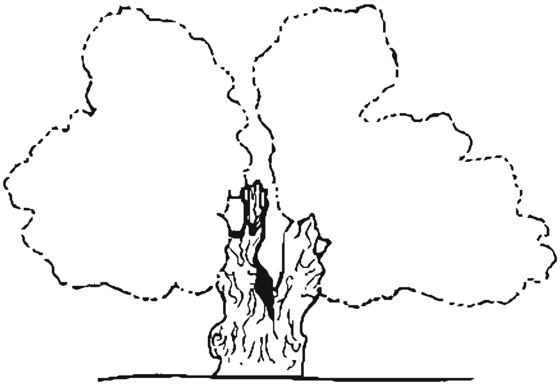


FIG. 3.4

In an over-mature but still living tree, various major classes of habitat(for saproxylic invertebrates) may be recognised:

a) loose bark and the bark/wood interface

b) dead wood

c) partly decomposed wood resulting from the actions of other saproxylics(including saproxylic fungi)

d) rot-holes

e) saproxylic fungi

f) the workings(i.e. burrows and cavities) of other saproxylics

g) tree humus

Each of these elements can have its own distinctive community of saproxylics. The saproxylic communities occurring in similar habitats in trees of the same species, but on different sites, will be differentiated by regional climatic differences. Similar habitats occurring in trees of different species found growing together will also carry different complexes of saproxylics, according to the tree species involved. These differences are maximal between deciduous and coniferous trees. Each physical feature, for example the dead branch, may exhibit differences in the saproxylics it supports, even according to its size and where it is located on the tree. Within one locality such differences are dictated by the humidity and temperature regime of the micro-climate of the particular feature involved, as well as by its biotic character. At some point in time, the biotic character of dead wood becomes as much dependent upon which saproxylics have occupied it previously, as upon other factors. So the communities of saproxylics occurring in different parts of a tree can become further and further differentiated as the decomposition process proceeds. In the same way, the communities of saproxylics found in fallen, dead, timber differ from those on living trees. In many cases, by the

Similarly, Swift et al(1976) showed that dead branches on living trees have largely been decomposed before they reach the forest floor.

3.2.1. Bark and the subcortical zone

There are saproxylic invertebrates which live only within the bark of old trees, and many more that occur only directly beneath it in the subcortical zone. They often have one distinctive morphological feature in common - they are dorso-ventrally flattened. The larvae of pyrrhochroid beetles and all developmental stages of the aradid bugs (fig. 3.5) are good examples. A number of species of Aradidae are restricted to under-bark habitats on trees which have been killed by fire, particularly fire-killed Pinus species. One of the blue-stain fungi of conifers, Ceratocystis minor, plays a role in increasing the accessibility of the under-bark zone to other saproxylics by means of the "pressure cushions" it forms as part of its fruiting process. These pressure cushions first separate xylem from phloem and then split the bark open, in this way making not only space for development of its fruiting bodies but also entry points to the sub-cortex. Saproxylic insects which bore through the bark to reach the wood beneath also provide entry points to the subcortex in the process.

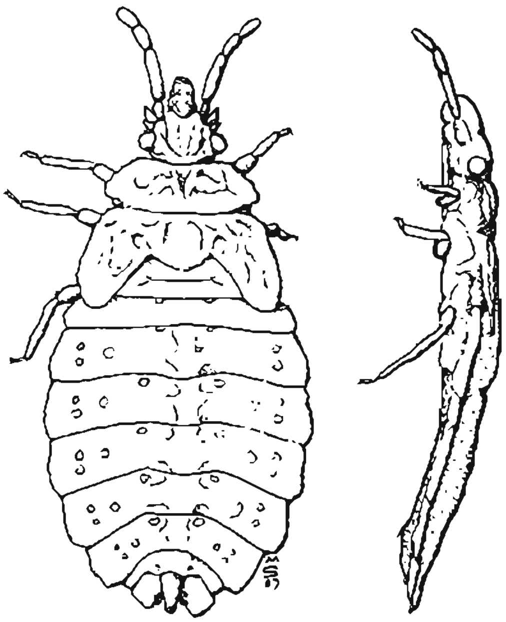


FIG. 3.5: Aradus, nymph / larve

Some saproxylics, such as Carabus intricatus, are dependent upon the loose bark of dead trees as much for shelter as for food. This beetle also specialises in predation of molluscs that are using under-bark cavities for shelter. Various spiders specialise in use of the under-bark habitat. Among the largest of them are Araneus umbraticus and Segestria florentina. Another arachnid group which contains a number of species largely restricted to the subcortical zone is the Pseudoscorpionoidea.

The subcortical zone of a fallen tree that has retained its bark possesses a more uniform and higher humidity than would be found if the bark were absent. This gives rise to a more diverse fauna than that found in debarked timber. In a forest otherwise too dry in some season to support them, organisms such as molluscs may shelter under the bark of such timber in large numbers. In the winter, the sub-cortical zone is also important in providing hibernation sites. Inevitably, there are species that exploit such concentrations of potential food. One snail-killing fly, Pherbellia annulipes, is rarely found away from rotting logs in ancient beech(Fagus) forest.

from rotting logs in ancient beech(Fagus) forest.

Sap extruding through the bark provides a particular bark zone habitat. Sap runs on moribund trees, whether induced by mechanical damage, fungal lesions or the wood-boring activities of other saproxylics. are inhabited by a specialized fauna, including the larvae of various Diptera(e.g. ceratopogonids, drosophilids, Aulacigaster etc.) and Coleoptera (e.g. the buprestid genus Epuraea).

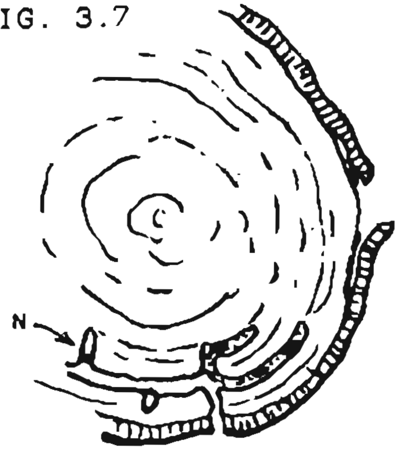
3.2.2. Dead wood and partly decomposed wood

The most easily identified category of saproxylics is that comprising species whose larvae feed directly on dead or partly decomposed wood, typified by the jewel beetles (Buprestidae), longhorn beetles (Cerambycidae) and certain click beetles (Elateridae). The tunnels of insects like these may be found in twigs, branches, trunks, stumps, logs and roots. Prionus coriarius is an example of a large cerambycid with tree-root-mining larvae. In contrast, the larvae of the cerambycid Mesosa nebulosa occur in dead branches on living oaks. Similarly, larvae of various Anthaxia species develop under the bark of conifers, while those of some of the species of another buprestid genus, Agrilus, develop in twigs and small dead branches of various deciduous trees. Many of the beautiful red click beetles of the genus Ampedus may only be found as larvae in the red-brown, powdery wood of timber previously attacked by brown-rot fungi. The larvae of some of them are predators of the larvae of other saproxylic beetles found in this habitat, others use the part-decomposed wood itself. In the wood of conifers killed by forest fires are to be found the larvae of the jewel beetle Melanophila cyanea. In warm, dry forests along the Southern edge of Europe, dead roots and stumps of trees may be broken down by the activities of one or other of the few termite species indigenous to the region.

The dying and dead wood of trees freshly brought down by wind-throw is quickly colonised by primary saproxylics. Even this relatively homogenous substrate is differentiated into a series of habitats defined by variations in the wood micro-climate. Logs with one end in the sun and propped up off the ground can develop one fauna in the raised portion exposed to the sun(e.g. buprestids such as Chrysobothris), another in the cooler, upper side of the shaded portion(e.g. the cerambycid Monochamus) and a third in the damper, lower side of the shaded portion(e.g. the cerambycid Asemum) in contact with the ground (see Graham,1925). In damp, part-rotted, timber of dead trees fallen for some years occur the larvae of some of Europe's largest tipulid Diptera, including those of the exotic-looking black and yellow Ctenophora species. Beneath the bark of rotting conifers that are still standing, though long-dead, can be found both adults and larvae of the three rhysodid beetles known from Europe. Many of the saproxylics found in the dead wood of these chandelles do not occur in fallen timber, and vice versa (figs. 3.6 - 3.11). There is similar differentiation of the faunas of damp and dry rotting logs. The fauna of timber which has fallen to lie part-submerged in water represents an extreme of this phenomenon.

FIG. 3.6

FIG. 3.7



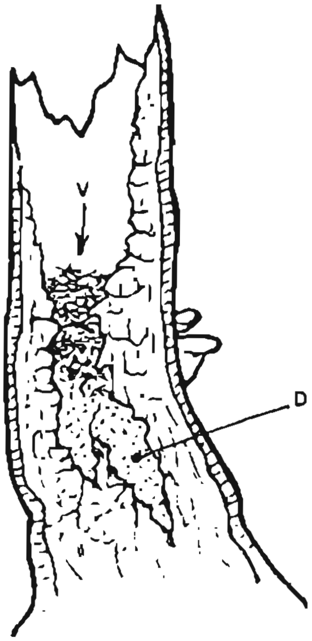


FIG. 3.8

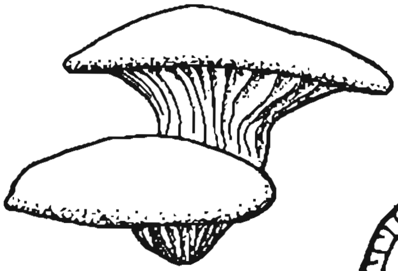


FIG. 3.11

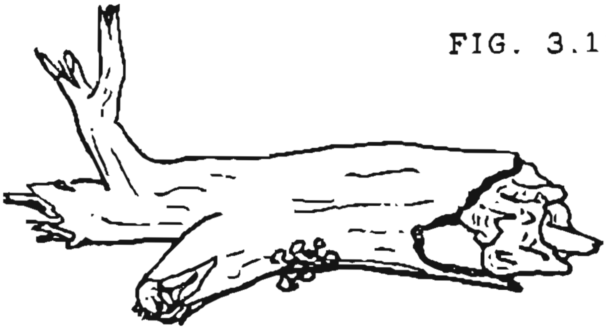


FIG. 3.9

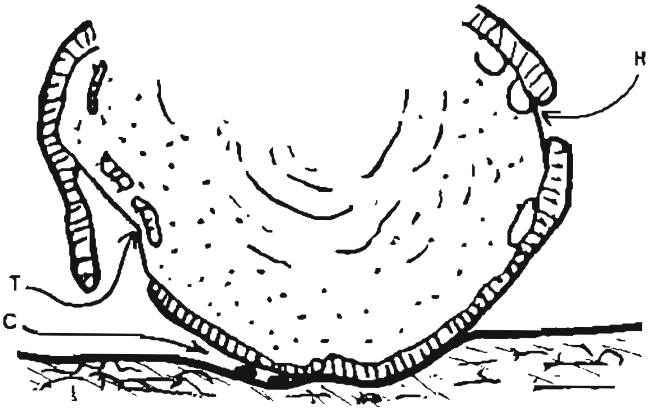


FIG. 3.10

FIGS. 3.6–3.11: Standing, dead trunks, or chandelles (Fig. 3.6), are drier than fallen trunks (Fig. 3.9). Beetle workings (Fig. 3.7) in dry wood may provide nest-sites (N) for crabronid wasps. Moist wood (Fig. 3.10) may support tipulid larvae (T) and provide for hibernacula (H) of various insects. Molluscs and ground beetles (C), use rotten logs for shelter. The cavities within a chandelle are usually dry (Fig. 3.8), with a core of wood dust (D) overlain by a layer (V) of wood fragments, twigs and leaves. This material provides habitat for many secondary saproxylics. Others depend upon saproxylic fungi or their fruiting bodies (Fig. 3.11).

There is a distinct succession observable in the occupancy of rotting wood by saproxylics. This relates principally to the stage the wood has reached in the decomposition process and is considered in more detail in Chapter 4, section 4.3. Most of the invertebrates specialising in the use of rotting wood habitats decrease in numbers as the humification phase (see 4.3.3.) comes to dominate. But there are a few, notably the larvae of click-beetles such as *Anostirus parumcostatus*, which occur particularly in well humified wood.

The burrow-making activities of many larger saproxylics, like the larvae of wood-wasps and cerambycid beetles, makes the presence of these organisms obvious. But there is a host of smaller saproxylic invertebrates whose role in breaking down dead and rotting timber is at least as important. Prominent among these smaller saproxylics are members of particular families of Acari, such as the Phthiracaridae, or box-mites, and rhabditoid nematodes. As with many of the larger forms, the habitat requirements of these various species of wood-boring mites etc. can be quite subtle(see Trave & Duran, 1971) and give rise to complex communities (Athias-Binche,1977, 1979; Wallwork, 1974).

Some old-forest invertebrates tunnel in dead wood to provide themselves with nest-sites, rather than food. The magnificent semi-colonial bee *Xylocopa violacea* is an example, choosing dead branches for the purpose. Ant species, particularly of the genus *Camponotus*, make similar use of fallen timber. Other ants, noteable among them being *Lasius brunneus* and *L.fuliginosus*, make their nests in dead wood on living trees. In old trees, their nests can be very large and support a diversity of commensals and predators. The larvae of the ant-lion *Dendroleon pantherinus* occur only in old trees,in association with such tree-living ants. The larvae of a peculiar and now extremely scarce soldier-fly, *Clitellaria ephippium*, is nearly always found in association with the ant *Lasius fuliginosus*, which characteristically nests at the base of ancient trees, though it is sometimes found elsewhere.

3.2.3. Rot-holes

Rot-holes and tree cavities develop as the dead wood is processed by the combined action of fungi, invertebrates and micro-organisms. A tree cavity carries its own distinctive fauna, made up of organisms that caused it(and which continue to enlarge it), others that arrive to predate them and yet others that use habitats created within the rot-hole by the accumulating debris and the rejectamenta of the diversifying saproxylic community. The different saproxylics each occupy their own niches in the diversifying dead-wood environment created (fig. 3.12). Some rot-holes will be dry, others damp. In some, rain water trickling down the trunk accumulates, mixed with tree exudates, to form pools of water which persist through all or most of the year(fig. 3.13). In different tree cavities, the various saproxylics will each be found where the condition of the physical environment is appropriate to them (figs. 3.14 - 3.15). Major tree cavities may develop within the trunks of old, living trees, rendering a section of the trunk hollow.

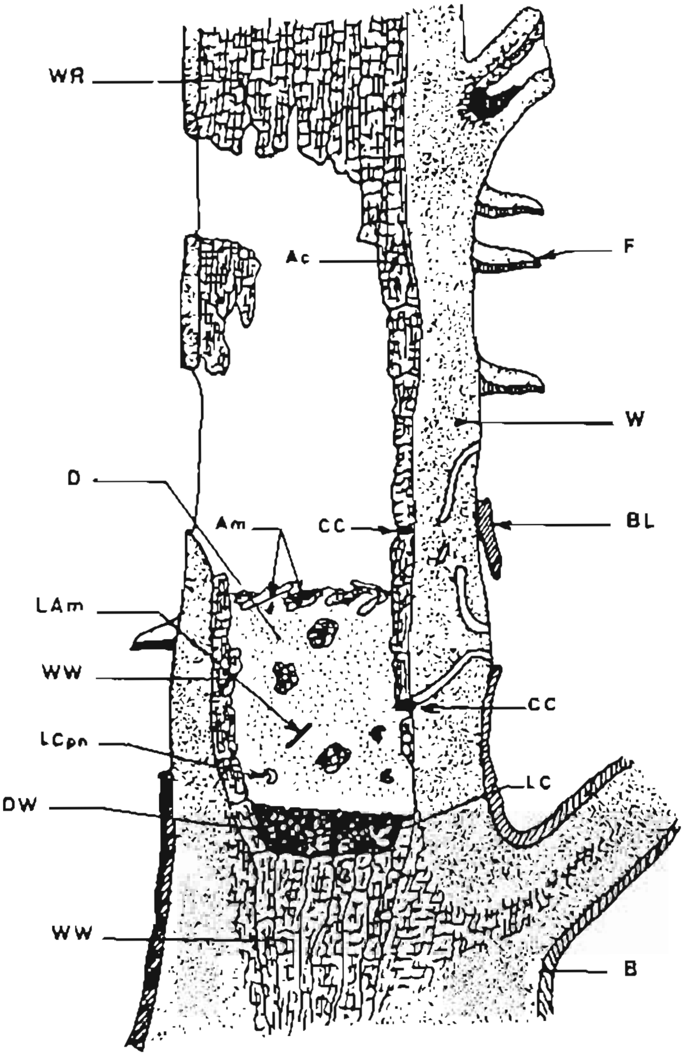


FIG. 3.12: Dead section of tree with large trunk cavity, showing the distribution of various saproxylic beetle larvae. Elaterid larvae (Am) and cetoniid larvae (LC) move to different situations when about to pupate (LAm, LCpn). Larvae of the two elaterid species involved (Ac, Am) occupy different types of decayed wood / Partie mort d'un arbre comportant une vaste cavité dans le tronc et répartition des larves de diverses espèces saproxyliques. Les larves d'elaterides (Am) et de cetoniides (LC) se déplacent au moment où elles vont se transformer en nymphes (LAm, LCpn). Les larves des deux espèces d'elaterides représentées (Ac, Am) occupent differents types de bois pourris.
Ac = Ampedus cardinalis, larva / larve; Am = A.megerlei larva / larve; B = bark / écorce; BL = loose bark / écorce partiellement détachée; CC = pupal cells of cetoniid larvae / cellules de nymphes de larves de cetoniides; D = dry wood dust / poussière de bois sèche; DW = damp, glutinous wood dust / poussière de bois humide glutineux; F = Polyporus sulphureus; LAm = A.megerlei, prepupal larva / prépupe; LC = cetoniid larva / larve de cetonide; LCpn = prepupal cetoniid larva / prépupe de cetonide; W = dead wood / bois mort; WR = red, rotten wood (attacked by brown-rot fungi) / bois pourri rouge (attaqué par des champignons lignicoles); WW = moist, red, rotten dead wood / bois mort pourri rouge, humide.
(after / après Iablokoff, 1943)

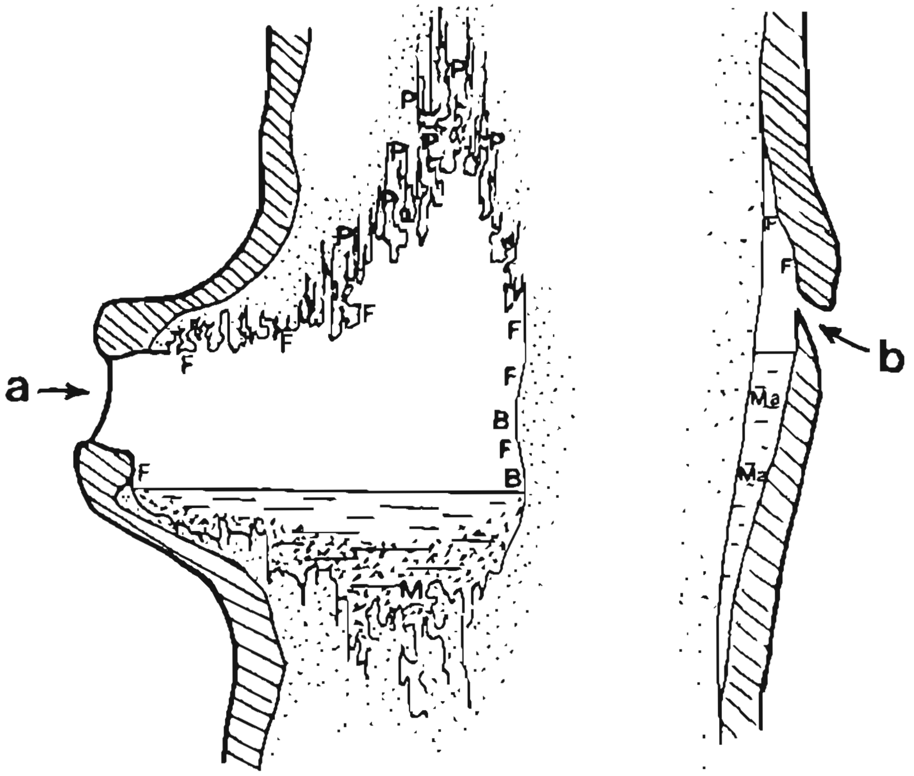


FIG. 3.13: Water-filled tree cavities, showing distribution of some associated fly larvae / Cavités emplies d'eau et répartition de certaines larves de diptères

a) wet cavity with large entrance hole. Wet wood in the roof of the cavity, attacked by saproxylic fungi, is inhabited by Phaonia larvae (P); the wall of the cavity above water-level is inhabited by Brachyopa (B) and Fannia (F) larvae, while the water-filled pocket contains aquatic ceratopogonid and Myathropa (M) larvae / cavité humide à grande ouverture vers l'extérieur. Le bois humide du plafond, attaqué par des champignons saproxyliques, est habité par des larves de Phaonia (P), et la paroi située au-desus du niveau de l'eau est habitée par des larves de Brachyopa (B) et de Fannia (F) tandis que la poche emplie d'eau contient des larves aquatiques de ceratopogonides et de Myathropa(M)

b) wet sub-cortical pocket reached via a narrow crack in the bark, with Fannia (F) larvae on the walls and Myolepta (Ma) larvae in the water / dans la poche sous-corticale accessible par une étroite fissure dans l'écorce se trouvent des larves de Fannia (F) sur les parois et de Myolepta (Ma) dans l'eau

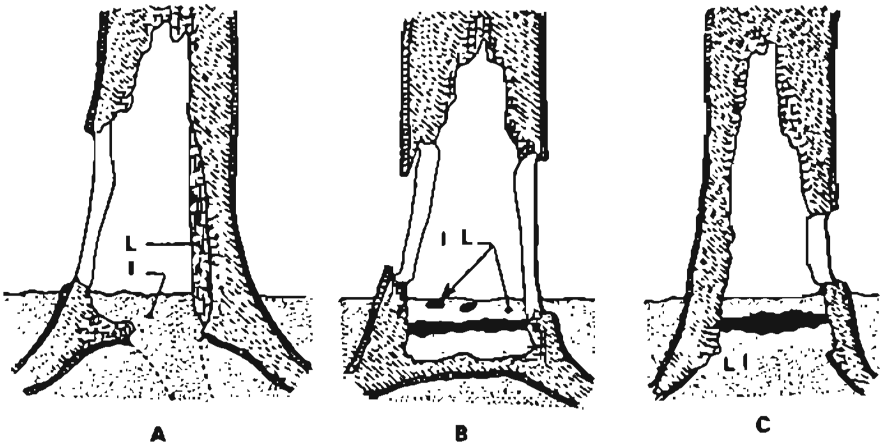


FIG. 3.14: Types of dry, tree-base cavity found in old beech (Fagus), showing location of larvae of particular elaterid species under different conditions / Types de cavités sèches trouvés à la base des vieux hêtres (Fagus), montrant des larves de certaines espèces d'elaterides dans différentes situations.
A = tree with dry cavity / arbre comportant une cavité sèche;
B = tree with damp cavity / arbre comportant une cavité humide;
C = tree with wet layer in cavity / arbre dans la cavité duquel se trouve une couche humide; I, L = elaterid larvae / larves d'elaterides; solid black denotes wet wood dust / les zones noires sont constituées par une poussière de bois humide

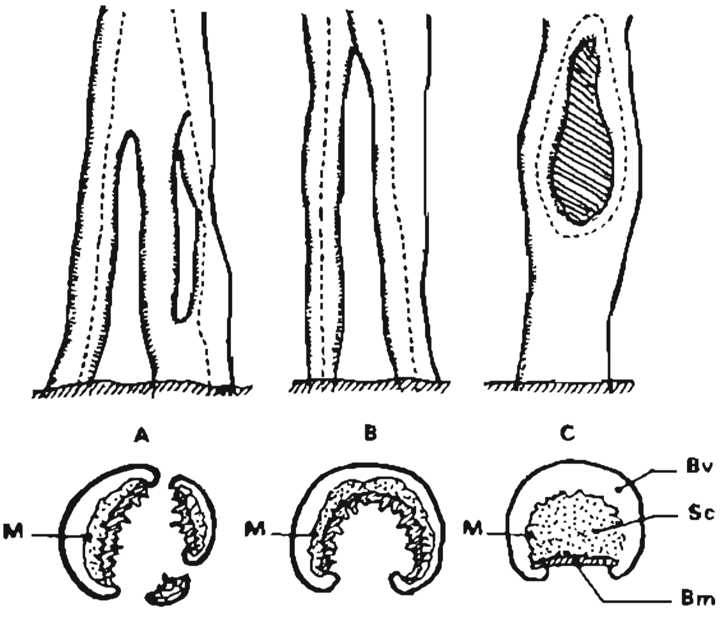


FIG. 3.15: Larvae of other species prefer the walls of cavities. On the walls of open cavities (A, B) there is only a thin layer of wood dust, behind a protective screen of dead wood left in situ by saproxylics. In a closed cavity (C) the entire cavity remains filled with wood dust, behind a thin plug of dead wood / Les larves d'autres espèces préfèrent les parois de cavités. Si la cavité est ouverte (A, B), il n'y a qu'une mince couche de poussière de bois, recouverte d'un écran protecteur formé par du bois mort et laissé sur place par les saproxyliques. Fermée (C), elle est entièrement remplie de poussière de bois et obturée par un fin bouchon de bois mort.
Bm = dead wood / bois mort; Sc = wood dust / poussière de bois;
M = elaterid larvae / larves d'elaterides
(after / après Iablokoff, 1943 & Leseigneur, 1972)

One of the sites at which tree cavities most frequently begin is where a branch has broken off close to the trunk. Dry rot-holes have faunas different from wet rot-holes and usually the walls, ceiling and floor of a rot-hole each are used by rather different assemblages of organisms(figs. 3.12 - 3.15). In rot-holes containing standing water, species with fully aquatic developmental stages occur, specialised to exploit the rot-hole environment and not found elsewhere. Dipteran larvae of the hoverfly genera Callicera and Mallota, and various mosquitoes, are examples. Rot-hole faunas include specialised predators and parasites, dependent upon the other rot-hole inhabitants. Thus fly larvae of the dolichopodid genus Systenus are virtually confined to rot-hole pools, where they predate larvae of ceratopogonid midges.

In natural forest conditions a typical component of the dry, hollow-trunk fauna is the honey-bee, Apis mellifera, which must have been largely dependent on hollow trees for nest sites throughout most of its European range. But for the provision of artificial nest-sites by man, one can only conclude that the honey bee would by now have virtually disappeared from most of Europe, along with the other invertebrates dependent upon old trees. Certainly, another tree-hole nesting aculeate, the hornet, Vespa crabro, has dwindled with the forests.

Height above the ground and size of entrance hole can both affect the constitution of a tree-cavity fauna, in addition to more obvious factors such as degree of dryness or the tree species involved. Standing-water rot-holes are largely confined to aged, living trees and although they may persist in chandelles they rarely do so for long.

3.2.4. Saproxylic fungi

The interaction between saproxylic fungus and saproxylic invertebrate may be no more than that the activities of the fungus provide access to the tree's tissues for the invertebrate, or vice versa. But for many saproxylic invertebrates the cavitated and part-decayed wood resulting from fungal attack is their preferred habitat, representing both living space and food source. Others feed on the fungal hyphae or fruiting bodies. For some, the fungal fruiting bodies themselves provide both shelter and food. This is particularly so in the case of the Polyporaceae, whose large brackets(the fruiting bodies) provide self-contained environments for quite complex communities of organisms. Cecidomyiid, drosophilid, keroplatid and lonchaeid flies, ciid and mycetophagid beetles, aradid bugs - these and their associated predators and parasites all utilise saproxylic fungi as habitat. The larvae of the largest European keroplatid, Keroplatus tipuloides, now excessively localised in its European distribution, live beneath the brackets of Fomes fomentarius, upon whose spores they feed. The ciid beetle Cis boleti inhabits the brackets of Polystichus versicolor, while C.bilamellatus prefers Polyporus betulinus. From such preferences, widely divergent assemblages of species can come to inhabit adjacent dead trees in the same forest(see, for example, Paviour-Smith, 1960). Just as there are saproxylic fungi that specialise in the use of dead branches, and others that prefer dead roots, or the cambial layer, or heartwood (see Frankland et al, 1982, Plank, 1983), so too there are saproxylic invertebrates that exploit the fungi characteristic of each of these different parts of the tree. The inter-relationships between fungus and invertebrate have in some instances become extremely complex, the morphology of some beetles becoming specially adapted to provide storage for symbiotic fungi that are then carried by the insect wherever it goes, so that colonies of its symbiont can be established when the beetle sets up a new colony. Various saproxylic fungi are also adapted to maximise chances of being transported to appropriate new habitat by saproxylic invertebrates, a frequent device being the development of sticky spores that adhere to the invertebrates on contact.

3.2.5. The workings of other saproxylics

For a host of other species, the debris-filled tunnels and cavities left behind by the activities of primary saproxylics represent easy access routes into the midst of supplies of their preferred food. For some, like clerid beetles, the food preferred is other occupants of the tunnels. For others, it is the fragments of part-denatured wood represented by the faeces of the primary saproxyilics, or the fungi and micro-organisms also growing on these wood fragments, or fungi which have themselves used these tunnels to gain access to the wood and are now spreading from the walls of the tunnels into the surrounding timber. Trees supporting strong colonies of the goat moth, *Cossus cossus*, or of the cerambycid *Cerambyx cerdo*, develop diverse communities of secondary saproxylics dependent upon the burrowing of the larvae of these insects. The tunnels of wood-boring species, especially those just beneath bark, are also critically important to the survival of a series of more temporary residents, which use them as hibernation sites wherein to pass the winter months(see, for example, Larkin & Elbourn, 1964, Paviour-Smith & Elbourn, 1978). In the summer, these same workings can be important as nesting sites for particular hole-nesting wasps and bees, with their entourage of dependent parasites and predators, like the fly genus *Eustalomyia*.

The activities of the secondary saproxylics result in the production of habitats appropriate for yet other species and so on, until a tree humus is produced. During the course of this process, the assemblages of saproxylics inhabiting adjacent trees, or even adjacent parts of the same tree, can come to differ markedly from one another.

3.2.6. Tree humus

Progressively, as it is used by a succession of invertebrate, fungal and microbial saproxylics, dead wood is converted into a fine, red-brown dust, quite appropriately referred to as tree humus(Kelner-Pillault, 1967). When damp, it has a loose-textured crumb structure and if thoroughly wetted it becomes a slightly sticky paste. By the time it has reached this stage, a rotting log on the forest floor is inhabitated by soil litter-layer and humus-layer organisms, as well as by organisms proper to the wood decomposition process itself.

On a living tree, tree-humus begins to accumulate in tree cavities almost from the time of their inception. But tree cavities that are open to the outside (and many tree cavities are open, particularly the larger ones) come to contain a more heterogenous mix of materials than is to be found sealed beneath the bark of a log rotting on the forest floor. Undermined by the activities of burrowing beetle larvae pieces of hardly decayed wood drop from above into these cavities. The wind blows into them part of the annual leaf-fall of the forest. Twigs, nuts and bits of bark fall in. A varied assortment of plant and animal debris can be brought in by tree-hole nesting birds. A jumbled mass of tree humus, of more than a metre in depth, structurally more varied and nutrient-enriched in comparison with its rotting log counterpart, can in this way come to occupy a large tree cavity in an old tree. In deciduous trees, like chestnut and oak, the upper layers of this sort of material provide habitats for species such as the tenebrionid Helops coerulea, the cucujid beetle Prostomis mandibularis and larvae of chafers like Gnorimus octopunctatus. Deeper in this material occur click beetle larvae, Cardiophorus species and Elater ferrugineus included. Under equivalent conditions in beech tree humus occur the larvae of the chafers Gnorimus nobilis and Osmoderma eremita, while in pines is found the lycid Dictyoptera aurora. These tree humus inhabitants comprise very particular communities which do not occur elsewhere. They vary one from another according to the tree species involved, the annual humidity and temperature regime of the cavity and cavity age.

Wood in an advanced state of humification is progressively invaded by soil organisms, and in particular by soil litter-layer inhabitants. Their habitat requirements are reviewed by Wallwork(1970, 1976). Many of these species could persist successfully in an absence of the rotting timber.

3.3. Saproxylics away from wood

There are saproxylics which pass their entire life cycle within decomposing wood, but most of them leave that habitat for some phase of their life history. Usually, it is the adult phase which is passed elsewhere. More often than not, the adult phase is used for dispersal, it being the adult female that searches for new supplies of wood in a condition appropriate to provide a food supply for the following generation. Away from the decomposing wood the adults have different habitat requirements. In particular, the adults of many of the insect species which develop in wood require flowers, to provide the pollen and nectar upon which they depend for food. In many cases, the pollen is a vital protein source without which egg maturation cannot be achieved. It is probable, though unproven, that the presence of flowers, especially flowering trees that flower when the adult insects are on the wing, are as critical to the survival of diverse saproxylics as are appropriate larval habitats in the rotting timber. The adults of many cerambycid beetles may only be conveniently found at flowers, while they feed.

The adults of other saproxylics feed at sap runs, hoverflies such as certain *Brachyopa* species and *Sphiximorpha subsessilis* being rarely seen elsewhere. The large, hairy and rather fearsome-looking adults of the robber-flies *Laphria ephippium, L.flava* and *L.gibbosa,* whose larvae predate other saproxylics within rotting wood, are also predatory as adults. But the adult habitat is the open forest, where they lie in wait, motionless on a tree trunk, until some hapless insect flies past. A rapid, darting flight to snatch their prey from mid-air provides them with their food supply.

More temporary members of the saproxylic community, such as the organisms which, like the ground beetle *Pterostichus oblongopunctatus,* depend upon dead wood to provide hibernation sites, may have little to do with dead wood at other times of the year. *P.oblongopunctatus* forages in the forest litter layer. The hornet(*Vespa crabro*) which hibernates beneath loose bark also makes its nest in hollow trees. The various wasp(*Vespula*) species frequently to be found hibernating in the same situation do not usually nest in trees, but close to the ground in more open terrain.

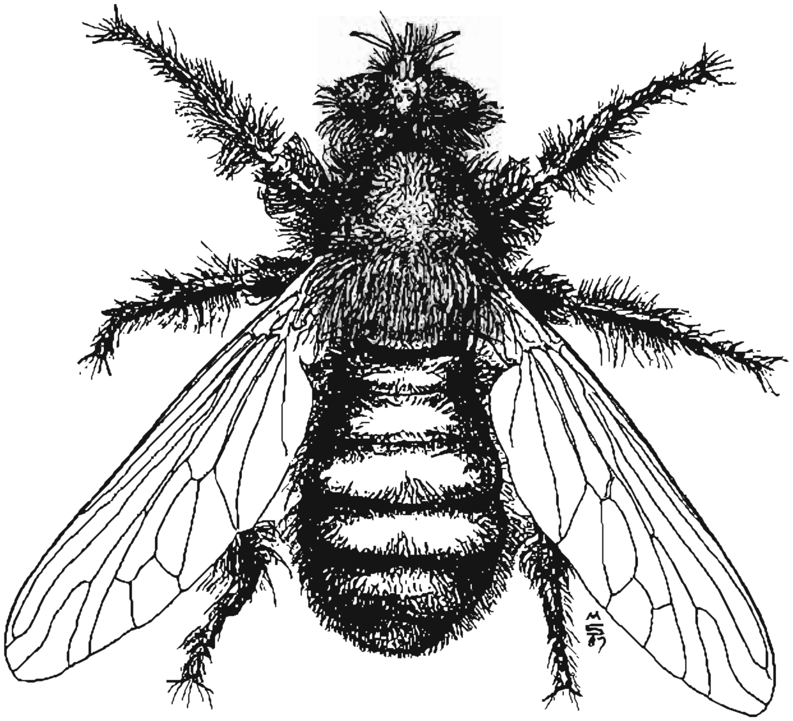


FIG. 3.16: *Laphria ephippium*. The larvae of this robber fly live in the dry wood of standing, dead beech (*Fagus*), where they predate the larvae of other insects.

4. THE ROLE OF SAPROXYLIC INVERTEBRATES

4.1. The ecological cycle

A feature of fundamental significance to the biosphere is that energy and nutrients, introduced into an ecosystem through the action of photosynthetic plants, are used and reused many times before finally leaking away or becoming trapped in some untappable form. The process of cycling and recycling energy and nutrients, popularly dubbed the ecological cycle, can be conveniently sub-divided into three sectors of activity. The first sector, that of primary production, is the province of the photosynthetic plants, through whose actions the cycle is initiated. The second sector, that of secondary production, is the province of many animals, both vertebrate and invertebrate, which convert living plant tissue into animal tissue and, through predatory action, repeatedly use the contained energy and nutrients to produce further animal tissue. The third sector, that of re-cycling, is the province of a miscellany of organisms, dominated by invertebrates, fungi and micro-organisms. These organisms may conveniently be referred to en bloc as saprophages. Through their activities, energy and nutrient contained in dead animal and plant tissue, or animal faeces, are re-introduced to the ecological cycle in the form of live saprophages. They also mediate the re-introduction of further nutrients from among the break-down products they do not use themselves, as organic and inorganic chemicals taken in by plants. Among the saprophages occurring in forests are the saproxylics.

4.2. Energy and nutrient recycling in forests

A singular feature of forests is that upwards of 30% of the plant biomass produced annually is in the form of perennial, woody, tissue. This is in sharp contrast to the situation in grassland, where only a minute fraction of the plant biomass produced one year persists into the next. The recycling of woody tissues poses particular problems for saprophages, giving rise to the specialised fauna and flora of saproxylics upon which attention is focused in the present account.

In natural forest, the trees otherwise removed by human action all die in situ and their constituent nutrients and energy find their way back into the forest ecosystem through the action of saproxylics. It is difficult to imagine this in the Europe of today, where there is hardly a forest to be found in which any significant proportion of the standing crop of trees is allowed to die naturally and decay on site. In one of the few forests in which trees have been left to die undisturbed, Dajoz (1974) estimated there were 6 tonnes per hectare of dead wood. The long-term effects of repeatedly exporting nutrients and energy from the forest ecosystem, by taking away the standing crop of trees whenever it is deemed harvestable, seem to be little understood. Detrimental effects upon the structure of the humus layer of forest soils are recognised (see Agren, 1986) and an increasing acidification of their upper horizons in general is suspected.

The woody tissues of a moribund tree are by no means a homogeneous phenomenon to a saproxylic organism, and the multiplicity of habitats, each with its own fauna of saproxylics, that can be represented among the trees of a forest, are considered in Chapter 4 of this account. Interestingly enough, no vertebrate animals have evolved to use dead wood as a source of food, so invertebrates, fungi and micro-organisms are virtually the only organisms involved. One small group of vertebrate saproxylics which can be recognised are the Picidae, the woodpeckers, represented in Europe by some ten species. Their place in the saproxylic complex of Europe's forests is as specialist predators of wood-feeding insects, and the rarity of some of Europe's woodpeckers today is a reflection of the extent to which populations of saproxylic invertebrates have been reduced.

Estimates of the contribution made to the energy and nutrient budget of a forest, by the recycling of dead wood, have, unfortunately, mostly been based on data gathered in commercial forestry crops, which bear little resemblance to natural forest because the quantities of dead wood available for recycling are minimal in commercial plantations. However, from figures provided by Swift(1977) it can be concluded that, in natural forest, the quantity of plant nutrients recycled annually through the activities of saproxylics is roughly equivalent to 50% of that recycled from the annual leaf fall. But, in contrast to the fate of nutrients recycled through annual leaf fall, nutrients recycled through the actions of saproxylics do not quickly find their way back to the the plant root zone for re-use by forest vegetation. They instead become incorporated into the saproxylic biomass, through which they may pass repeatedly, via the actions of predatory and fungal feeding members of the saproxylic complex. In similar fashion, saproxylics may be absorbed into the secondary production sector. The passage of nutrients from a dead tree to saproxylic invertebrates ensures not only that these nutrients are recycled back into the ecosystem, but also, due to the mobility of the invertebrates, that they are disseminated through the forest rather than remaining concentrated where the tree died.

The low concentrations of available nutrients found in wood, coupled with the fact that at any one time only a low density of saproxylics may be found in it, has given rise to under-estimations of the saproxylic biomass it can support. In reality, because of its high energy content, wood provides a food source adequate to ensure survival for long periods, whilst saproxylics search out sufficient nutrient to complete their development (saproxylics have characteristically attenuated life histories in consequence), through their activities making more of the trapped nutrients bith physically and chemically accessible to each other (Dowding, 1976). So, successions of saproxylics inhabit the same wood, together totalling a much greater biomass than can be observed at any one time in the succession.

4.3. The process of wood decomposition

Although the particular saproxylics involved will depend on many factors, the decomposition process occurring within a log, branch or root of almost any tree tends to progress in the same general fashion under most conditions. Three phases can be recognised in the process:

a) the colonisation phase, during which the wood is invaded by primary saproxylics, which use the intact wood,

b) the decomposition phase, during which the primary saproxylics are joined by a host of secondary saproxylics, which use the product of the activities of the primary saporoxylics as food, or which feed on other saproxylics,

c) the humification phase, during which the saproxylics are progressively replaced by soil organisms, most of which feed on the bacteria and micro-fungi that play a dominant rôle in humifying the wood.

The overview of the decomposition process presented here is based largely upon Dajoz(1980) and Frankland et al (1982). Accounts of the sequence of events occurring in the wood of various trees under natural conditions are provided by Dajoz(1966, 1977), Derksen(1941), Kelner-Pillaut (1967), Krogerus (1927), Palm (1951, 1959) and Schimitschek (1953-54), whose studies were conducted in forests with highly differentiated saproxylic faunas. Other accounts, based upon less suitable localities, are difficult to interpret. For instance, Wallace(1953) studied decomposition of pine stumps at a location some hundreds of miles from the nearest stand of indigenous conifer woodland and in a part of Europe from which most conifer-inhabiting saproxylics are absent. Similarly, Fager(1968) and Larkin & Elbourn(1964) carried out work on decomposition of oak in woodland from which nearly all oak saproxylics were lacking.

4.3.1. The colonisation phase

In the colonisation phase, enfeebled or recently dead trees are invaded by certain saproxylic beetles armed with an ability to digest cellulose and jaws strong enough to enable them to gauge tunnels through the bark and into the still hard wood. Others among these pioneers specialise in the use of the cell contents of the tree's cambium and sapwood just beneath the bark, despite the presence there of elements of the tree's chemical defence system, still in operation. Wood-boring mites and fungi are also members of this "expeditionary force", carried in on the bodies of the beetles. Together, these organisms can be conveniently referred to as the primary saproxylics.

It is among these primary saproxylics that are to be found the few notorious conifer pests that are to be numbered among Europe's saproxylic invertebrates. Favoured by forestry practises of growing vast monocultural stands of the same few conifers throughout the continent, and of planting these trees so densely that many of them are under physiological stress sufficient to reduce the effectiveness of their defensive mechanisms, a small group of saproxylics, prominent among them the weevil Hylobius abietis and certain scolytid beetles, have expanded their ranges enormously. They are now found more or less wherever commercial conifer crops are grown. The particular scolytids involved, generally known as the bark beetles, are unable to establish populations in healthy conifers, but, in an unhealthy tree where the resin-producing mechanism is inadequate, can penetrate the bark and tunnel in the cambial layer without being overwhelmed. Within two or three years they build up dense colonies beneath the bark. Their activities further reduce the tree's vigour and provide access points (known to forest pathologists as "infection courts") and necrotic tissue suitable for colonisation by other saproxylics, both fungal and invertebrate. In this way a sick tree which nonetheless contained useable timber can be converted into a dead tree whose timbers are already part decomposed, and unuseable. But even bark beetles can only cause damage of economic significance over a rather narrow range of circumstances (Bevan, 1987). These scolytids are unusual among primary saproxylics, in that they do not possess cellulases and hemicellulases, which would enable them to digest parts of the cell walls of woody tissues. In consequence their activities are concentrated in the cambial zone, just beneath the bark, where the widest variety of cell contents is available as food.

Most bark beetles carry with them symbiotic fungi, the blue-stain fungi of conifers being examples. It seems that, for the beetle, the advantage of transporting the fungus with it is primarily that the fungus, as it spreads through the wood, provides a convenient supply of dying tissue for the beetle's larvae to feed on. But, in some instances, the bark beetle larvae also use the fungal spores as a food source. In one case in Europe, that of the elm bark beetles, an unholy alliance has developed between beetle and fungus that enables the beetle to invade healthy, living trees, due to the ease with which the fungus can overcome the elm's defensive reactions. The devastating effect this beetle/fungus association has had on Europe's elm population throughout the postglacial period is evident from the pollen record, with elms more than once virtually disappearing from the pollen spectrum. The last few years have seen a resurgence of this "dutch elm disease", which has again wiped out most of Europe's elms. The depredations of this fungus/insect double act have been regarded with a sort of superstitious awe by both informed and uninformed opinion alike and, however much it can be quite truthfully argued that only a handful of species, among the thousands of European saproxylics, are implicated as the perpetrators of this "crime against nature", this devastation of Europe's elms represents a serious obstacle to any attempt to gain a better public image for Europe's saproxylic flora and fauna.

Another group of scolytids, together known (perhaps rather aptly) as the Ambrosia beetles, have reduced the influence of their digestive limitations by carrying with them symbiotic fungi which can more rapidly digest the wood. The beetle larvae then eat the fungus growing in the burrows excavated for them by the adult beetles. This stratagem enables Ambrosia beetles to utilise the sapwood, employing their jaws to make burrows and brood chambers deep in the wood. The activities of Ambrosia beetles rarely kill trees, but their burrows can disfigure wood and act as entry routes for other organisms. In these circumstances, Ambrosia beetles can cause economic damage to commercial crops of trees. Species of the cerambycid genus Monochamus can cause similar problems. The symbiotic relationships existing between saproxylic fungi and saproxylic insects have interested both entomologists and mycologists and have been reviewed more than once, recently: see Crowson(1981), Dajoz(1980) and Dowding(1984).

The few pest species of scolytid are greatly outnumbered by other scolytids that are not of economic importance. Similarly, the Scolytidae, as a group, make up only a very small proportion of the European fauna of primary saproxylic invertebrates. Many of these primary saproxylics are beetle larvae. Prominent among them are various species of buprestid and cerambycid, whose larvae, like most primary saproxylics, possess both hemicellulases and cellulases (see Dajoz, 1968, Parkin, 1940), and so can make use of sapwood and heartwood, as well as the cambial layer. But there are fundamental differences between the hemicelluloses of conifers and deciduous trees and few of the primary saproxylics possess enzymes capable of digesting the hemicelluloses of both sorts. In consequence, it is particularly unusual to find a primary saproxylic which can inhabit the wood of both conifers and broad-leaved trees. Similarly, since moribund and freshly dead wood contains a maximum diversity and concentration of chemicals specific to the particular tree species from which it is derived, some of which deflect saproxylics and others of which require specialised treatment during digestion (Becker, 1971), many primary saproxylics exhibit considerable restrictions in the range of trees they may inhabit, whether conifers or broad-leaved species are involved.

Unaided, primary saproxylics among the fungi are dependent upon tree wounds to provide them with access to the wood. But many of them have sticky spores, rendering them liable to transport by saproxylic invertebrates. The invertebrates can use their jaws to dig through the bark and into the wood beneath. Both of these groups of saproxylics have come to take advantage of entry points established by the other, and both take advantage of mechanical damage caused by tree pruning, wind, snow, lightning etc. The tunnels of primary saproxylics like Ambrosia beetles, which exhibit brood care, are less available as through routes for colonisation than tunnels of cerambycid beetles which do not, because the Ambrosia beetles actively defend their tunnels against intruders and the fungi already installed there by the beetles reduce the chances of establishment of other fungi. But the tunnels of buprestid or cerambycid larvae etc. are ideal access routes. Secondary saproxylics can establish themselves on the part-decomposed wood fragments left behind in the tunnels from the feeding activities of the cerambycid larvae, and the tunnel walls are available for penetration by other primary saproxylics (see fig. 4.1). During the colonisation phase, the contributions made by saproxylic fungi and saproxylic invertebrates to the process of decomposing the timber are roughly equivalent in magnitude, although in any one piece of timber the role played by some particular species of fungus or invertebrate may dominate overwhelmingly.

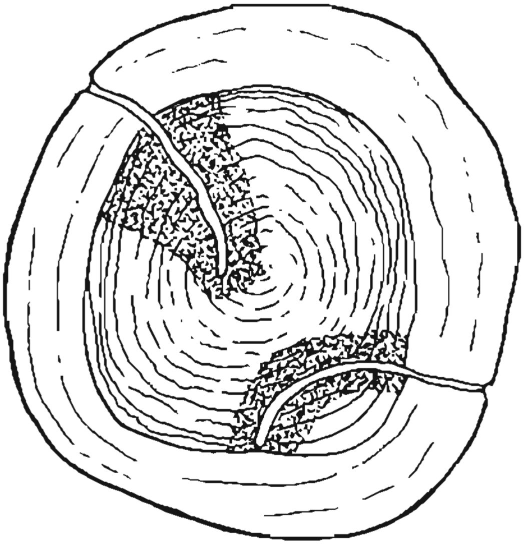


FIG. 4.1: heartwood decay (stippled) by a fungus, which entered the wood via the exit tunnels of a longhorn beetle (after Leach et al, 1937)

4.3.2. The decomposition phase

Saproxylics which are unable to tunnel themselves are dependent upon the primary saproxylics for provision of points of access to wood. Many saproxylics are also dependent upon primary saproxylics for processing the wood into some part-decomposed form. Another large and miscellaneous group specialises in feeding on either other members of the saproxylic invertebrate complex or on saproxylic fungi. By virtue of their dependence upon the primary saproxylics for preparing some element of their habitat for them, these species, whether saprophages, mycophages, predators or parasites, can be grouped as secondary saproxylics.

With the arrival of secondary saproxylics in timber, its decomposition both accelerates and diversifies, as more and more organisms become active in the wood and the part-decomposed product of the activities of primary saproxylics is utilised by secondary saproxylics species. The activities of the primary saproxylics continue, as they penetrate further into unused portions of the wood, and also increase, as more of them establish populations in the widening array of potential habitats. In a typical sequence reported by Crowson(1981), Mamaiev(1976) found that scolytids and cerambycids established themselves first, followed by pyrrhochroids, which were then joined by the lymexylids, themselves followed by lucanids. Dependent upon circumstance, the duration of the colonisation and decomposition phases will vary. But, in the erstwhile healthy wood of a wind-blown tree, for instance, the colonisation phase can be expected to take approximately two years from the date that the tree fell and died, in most parts of Europe. In the same wood, the decomposition phase can be expected to take somewhat longer, reaching completion some ten years after the tree fell. In an absence of saproxylic invertebrates, the decomposition phase (in these circumstances mediated by the fungi alone) is estimated to take twice as long(see Dajoz, 1980). Ehnstrom (1979) suggests that, in the colder climates of Northern Europe, the decomposition phase is characteristically much more protracted, taking in excess of 25 years even when both fungi and invertebrates are involved.

FIG. 4.2.: primary saproxylic, larva of a buprestid (after Viedma, 1963)

Among the invertebrate primary saproxylics, digestion of wood involves cell contents and the cellulose/hemicellulose component of cell walls. But the efficiency with which they digest the cellulose and hemicellulose is not very great. The larvae of a cerambycid, for instance, have been found to digest only some 10% of the cellulose content (Deschamps, 1954) of the material which passes through their gut. Their faeces thus remain rich in cellulose and, since through their chewing action cell walls have been ruptured in the ingested material, the remaining cellulose is more easily accessed than is the cellulose in undamaged wood. In the case of the primary saproxylic <u>Cossus cossus</u>, the goat moth, cellulose digestion is effected by symbiotic bacteria and fungi living within the gut of the goat moth caterpillar. These symbionts occur also in the caterpillar's faeces, though they do not spread into the surrounding wood.

Beetles and their larvae tend to predominate in the colonisation and decompositiuon phases in more or less dry timber and Dajoz(1980) suggests they can represent up to 95% of the total biomass of saproxylic invertebrates in a fallen tree. He estimates that, on average, during its development a saproxylic beetle larva can be expected to consume twenty times its weight at maturity. A stag beetle (<u>Lucanus</u> <u>cervus</u>) larva, which weighs approximately 1 gramme when fully grown, can thus be presumed to have ingested some 20 grammes of decomposing wood. In volume terms, this represents somewhat more than twenty cubic centimetres of wood.

Primary saproxylics among the fungi vary in the character of their digestive action, as do their invertebrate counterparts. The wood-stainers, including the blue-stain fungi (<u>Ceratocystis</u> species) which frequently live in symbiotic association with bark beetles (scolytids), do not digest cellulose but focus their attention on cell contents. They thus concentrate in the outer layers of wood just beneath the bark. In these characteristics they closely parallel the bark beetles themselves. The soft-rot fungi (which include a rather heterogenous assemblage of ascomycetes and fungi imperfecti) and the brown-rot fungi (which are basidiomycetes) digest cellulose by means of enzymes they secrete into the tissue through which they are growing. The brown-rot fungi can free cellulose from a wider range of locations where it is locked in cell-walls than can the soft-rot fungi, but in the process broadcast their enzymes more widely in the wood. The net outcome is that the brown-rot fungi tend to digest more wood than they can use themselves, and in so-doing provide a convenient food-source for other saproxylics, including various saproxylic invertebrates. The cellulose-degrading action of the brown-rot fungi is so thorough that following their presence in wood what remains of the structure is just a red-brown matrix of lignin. The availability of cellulose break-down products in such wood is sufficient to explain the concentrations of secondary saproxylics like elaterid and lucanid larvae that can be found there.

The basidiomycetes which comprise the white-rot fungi possess enzymes which can digest both cellulose and lignin and the break-down products of both processes are used by the fungi in their metabolism (Kirk & Fenn, 1982). The white-rot fungi are, then, almost the only group of primary saproxylics with the capacity to degrade lignin. There are lignin degrading bacteria among the secondary saproxylics and termites maintain populations of lignin-degrading protozoa in their guts but, so far as is known, the only part played by other saproxylic invertebrates in lignin break-down is that of comminution, the grinding action of their jaws rupturing the cell-walls and thus allowing access for fungus and bacteria alike.

FIG. 4.3: secondary saproxylic, larva and adult of the European rhinocerus beetle (Oryctes nasicornis)

Insect secondary saproxylics characterising the decomposition phase in wood are reviewed by Dajoz(1980). Prominent among the organisms concerned directly with the further decomposition of the wood itself, rather than with predation of other saproxylics or fungus-feeding etc., are larvae of elaterid, lucanid, and melolonthine beetles, anisopodid and tipulid flies. Where these organisms have been investigated they have proved to have cellulose-digesting capability, but mediated more often than not through the action of symbiotic micro-organisms. In some, like the lymexylid beetle Hylechoetus dermestoides, specially nurtured symbiotic fungi released into the wood by the insect carry out the necessary digestive action, the beetle larvae then feeding on the fungus and the wood. Low available nitrogen content is recognised as severely limiting the nutritional value of wood, and primary saproxylics are generally particularly efficient at extracting any nitrogen that is available. At least in the case of certain secondary saproxylics, like the larvae of lucanid and melolonthine beetles, the difficulty of extracting nitrogen is overcome by maintaining symbiotic, nitrogen-fixing bacteria within their gut (Dajoz, 1980).

More abundant than the species that re-use the part-decomposed wood are the predators of the primary saproxylic invertebrates and the fungivores which depend on the primary saproxylic fungi. Some secondary saproxylics feed on the part-decomposed wood for much of their time, but predate the larvae of other saproxylics as and when they come across them. Others actively search out the larvae of different species as food but augument their diet with the wood. The larvae of click-beetles (Elateridae), in particular, are known to adopt this sort of feeding regime and resort quite readily to cannibalism when food supplies are scarce.

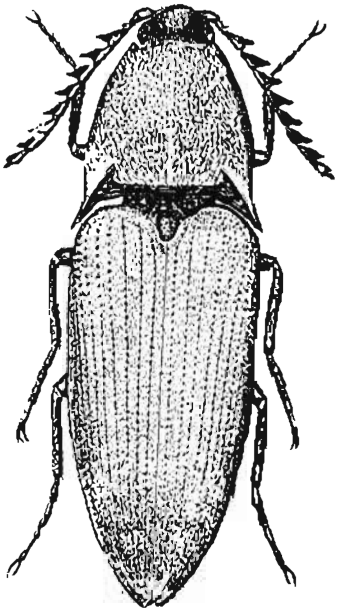


FIG. 4.4: a click beetle (<u>Elater ferrugineus</u>) with larvae predatory on those of other saproxylic insects (after Leseigneur, 1972)

4.3.3. <u>The humification phase</u>

As supplies of unused wood in a decaying trunk dwindle, so do the numbers of primary saproxylic invertebrates and their associated predators. Secondary saproxylics using the part-decomposed wood itself persist, their life-cycles becoming more attenuated as the nutrient value of their food supply decreases. By this stage the wood has been converted into a red-brown friable mass, composed largely of the faeces of saproxylics. The species typical of decaying timber are joined by others that can also be found away from trees, in the soil litter layer. Spring-tails (Collembola), woodlice (Isopoda), millipedes (Myriapoda), worms (Lumbricidae and Enchytraeidae), nematodes (Nematoda) and mites (Acarina), now come to dominate the fauna in much of the wood, within two or three years. Most of these organisms are microphages, feeding on the true tertiary saproxylics, the bacteria and micro-fungi which take the wood through the final, humification phase, of its decomposition. In this way the trunk becomes essentially an extension of the litter layer of the forest floor, which it crumbles into within a further few years.

Inevitably, in reality the process of wood decomposition rarely occur neatly packaged in time and space as it has been described here. For much of the time that a log is decaying, species representative of all decomposition phases will be present together. The same is true of the large trunk cavities not infrequently to be found in old trees, leading on occasion to perched communities of soil organisms occurring several metres above the ground surface in a living tree. The course of the decomposition process in wet tree holes is clearly somewhat different from the generalised pattern described in the paragraphs above. The larvae of a great number of different Diptera, many of them microphagous, others predatory, are confined to wet tree holes. Species representative of a surprising range of families are involved, but little can be said of them here because their roles in the decomposition process are as yet poorly defined.

4.4. Saproxylics and other organisms

Traditionally, the perceived significance of saproxylic invertebrates is that they comminute wood, transforming a large log into great quantities of small fragments, that are more easily colonised and used by both fungi and micro-organisms. The foregoing pages show that their contribution is actually more fundamental. Demonstrably, throughout the colonisation and decomposition phases the fungi and invertebrates form an effective and equal partnership, and exhibit a high degree of inter-dependence. In their partnership they are also aided and abetted by micro-organisms, which take over the dominant role in the last phase, the humification of wood.

The animal biomass represented by the saproxylic invertebrates of a natural forest can be seen to be significant in both the large number of species which contribute to its make-up and the boost it gives to secondary production. Saproxylic beetles, which are probably the best known saproxylic invertebrates, can comprise more than 30% of the beetle fauna of a forest. The combined list of saproxylic beetles recorded from the two French forests of Fontainebleau and Massane totals more than 1000 species (Dajoz,1965). Elton(1966), writing primarily on British woodlands (which have a depleted saproxylic fauna in comparison with continental forests), suggested that approximately 20% of all woodland animal species are either saproxylics or dependent upon saproxylics. Saproxylic invertebrates can, then, represent a major component of the genetic diversity that it is possible to conserve within a protected forest.

The relationships existing between saproxylic fungi and saproxylic invertebrates are clearly so intimate that the survival of members of the one group is frequently dependent upon the presence of members of the other. The implications of this inter-dependence to rates of wood decomposition in forests is obscured in much of the literature, since few accounts deal both with fungi and invertebrates. The role of the saproxylic complex(invertebrates plus fungi plus microbes) in differentiating the structure of natural forest also seems to have been largely ignored. But it is the saproxylics which create under-bark cavities and tree holes, upon which a significant number of forest bird species depend for nest sites and which tree-living bats need for roosting sites. The tree cavities and hollow logs saproxylics produce are equally important to other forest mammals, either as denning or hibernation sites. The woodpeckers form an integral part of the saproxylic complex themselves, dependent as they are upon saproxylic invertebrates for the major part of their food supply. These aspects of forest dynamics have recently been reviewed by Komdeur & Vestjens (1983), Voute (1983) and van Vuure (1983).

All other attributes of the saproxylic invertebrates have been overshadowed by the fact that entrepreneurs among them can take advantage of forests in poor condition, or "attack" neglected woodwork. In the perception of many people saproxylics are some sort of many-legged fifth column, skulking hidden beneath the bark of a superficially healthy tree, or the veneer of some piece of antique furniture, their presence being revealed only when the tree or table collapses in a pile of dust and their "evil work" is done. Meanwhile, the "silent majority" of the saproxylics, performing their age-old task of recycling wood through the forest ecosystem, fade into oblivion, their role unrecognised and their fate unremarked. Their contribution to the dynamics of natural forests has indubitably been generally under-appreciated, and recognition of the need to conserve them has dawned late. Many of them are of great beauty (see Stanek, 1984) or exhibit fascinating adaptations to their way of life. They are a part of Europe's heritage which, once lost, would be difficult to replace.

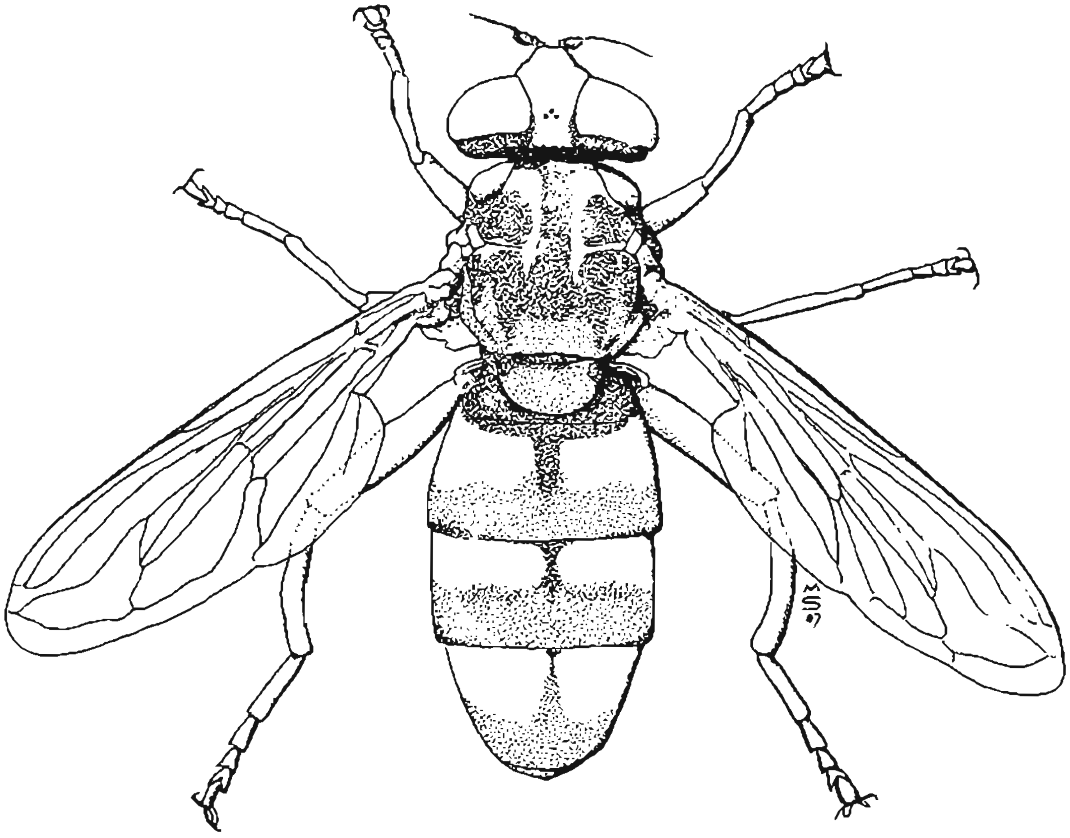


FIG. 4.5: *Milesia crabroniformis*, the largest European hoverfly. *Milesia* larvae live deep within moist, rotten wood at the base of moribund deciduous trees / Le plus grand syrphide d'Europe. Les larves de *Milesia* habitent creusés dans du bois pourri humide des troncs des feuillus sénescents, près des racines.

5. CONSERVATION OF SAPROXYLIC INVERTEBRATES

A rapid scan of the forests listed in Appendix 2 will show that but few of them have yet been put aside for conservation of nature: forests recognised by invertebrate zoologists as important nationally or internationally are more often than not omitted from similar lists drawn up by other specialists. It follows that a significant advance could be made towards securing the future of the invertebrate fauna of natural forest in Europe by establishing protected areas of adequate size within the forests listed in this report. However, there are many problems in the maintenance of viable populations of organisms that are not addressed by simply establishing reserves on appropriate sites. The objective of this section of the report is to highlight problems pertaining to the conservation of saproxylic invertebrates, and to suggest approaches helpful in overcoming these problems.

5.1. Establishment of forest reserves for protection of saproxylics

Remmert(1985) has discussed the problem of how large an area is needed for the re-establishment of natural forest conditions in a forest. The requirement to provide for the simultaneous existence of adequately-sized enclaves of all successional phases within the protected area dictates a minimum effective size of some hundreds of hectares. Hengeveld (1986) points to the need for more serious consideration of the problem of reserve size in relation to insect conservation in general. To provide for the continuous natural production of old and moribund trees, belonging to the long-lived tree species which carry the most diverse assemblages of saproxylics, it would be necessary to ensure the on-site presence of all the other successional stages, since these old trees represent the last phase in the successional cycle. When viewed in this light, most forests already being protected for nature conservation in Europe are clearly too small for natural forest conditions to be re-established in them and are likely therefor to serve other conservation objectives, unless their size can be increased. Some of these small protected forests have been set aside because they contain many old trees and their associated organisms. Enlargement of a protected forest which falls into this category is obviously highly desirable, so that an adequate area of younger trees is available to ensure the presence of a future supply of trees maturing towards senescence, as the present generation of old trees dies. In circumstances under which it is impossible to obtain a hectarage adequate to ensure natural production of old trees in sufficient quantity, in perpetuity, there is the alternative of managing the forest specifically to maintain the saproxylic flora and fauna, to the exclusion of other management objectives. Ways in which senility can be induced in trees and techniques for increasing quantities of dead wood in forests, as components of this type of forest management, are discussed below, in later sections of this chapter.

5.2. Site assessment involving saproxylic invertebrates

At present, procedures used for assessing the quality of sites for conservation purposes rarely involve survey of invertebrate groups. In particular, saproxylic invertebrates are rarely considered in survey work aimed at assessing the conservation value of forest sites. Similarly, surveys of saproxylics are rarely carried out as part of programmes aimed at defining management objectives for a protected forest. It has already been pointed out (see Introduction) that, unless survey data is available for some group of saproxylic organisms, there is little hope of gauging the health of the decomposer sector in a forest biotope. Inclusion of selected taxonomic groups of saproxylic invertebrates among those organisms routinely surveyed as part of site assessment procedures used on forest sites would help to provide the required data, and, in the process:

a) help to identify forests most suitable for use in attempts to re-establish natural forest conditions,

b) help to identify forests of importance for the conservation of saproxylic invertebrates.

Therefor, simply to include saproxylic invertebrates in baseline survey work carried out in forests would, in itself, represent an important step towards conservation of these organisms. The criteria used in deriving the species list employed for identifying the forests listed in this report are given in the Introduction. These criteria are compatible with those suggested by Speight(1986) for selection of insects to be used for site assessment in a wide range of biotopes. Various approaches to the use of invertebrates in site assessment are discussed in Usher(1986).

Insect groups which can be recognised as including many species with high potential as indicators of the presence of a well-differentiated fauna of saproxylic invertebrates in a forest include the following families, which have been used in compiling the species list in Appendix 1:

Coleoptera: Buprestidae, Cerambycidae,

Diptera: Syrphidae

A number of the other groups, although they comprise a large number of European species, include but few saproxylics. Into this category fall the following families:

Coleoptera: Carabidae, Scarabaeidae
Diptera: Asilidae, Dolichopodidae

There are also many small groups in which saproxylics occur, or whose species are all saproxylics. Some of these small groups were used in Appendix 1 and some were not. The following are examples:

Coleoptera: Boridae, Bostrychidae, Cleridae, Colydiidae, Cucujidae, Lucanidae, Lycidae, Melandryidae, Mycetophagidae,

Oedemeridae, Peltidae, Pythidae, Rhysodidae, Salpingidae, Scolytidae, Tenebrionidae
Diptera: Canthyloscelidae, Coenomyidae, Xylomyiidae, Xylophagidae
Hemiptera: Aradidae
Hymenoptera: Xiphydriidae
Lepidoptera: Cossidae

Finally, there are groups which include many saproxylics, but difficulties of determination preclude the use of many of the species. Examples are:

Coleoptera: Elateridae

Diptera: Cecidomyiidae, Keroplatidae, Mycetophilidae, Tipulidae

At this juncture it would be impossible to produce a definitive list of all the saproxylic insects occurring in Europe, let alone the European saproxylics in other invertebrate groups, and no such listing has been attempted here. Some notion of the scale of the task that would be involved can be gained from Dajoz's (1980) extensive survey of the invertebrate taxonomic groups that include saproxylic species. Stubbs(1972) suggests that in Britain alone there are nearly 1000 saproxylic invertebrate species, and the British saproxylic fauna lacks a majority of the European species belonging to various of the taxonomic groups particularly involved in wood decomposition, such as the longhorn beetles (Cerambycidae). Between them, Geiser (1983) and Holzschuch (1983) list nearly 400 saproxylic beetles alone, as threatened in Austria. Clearly, judicious selection from a narrow range of taxonomic groups would usually provide a basic list useful in identifying forests of importance at national level. The only account in which an attempt has been made to produce such a list of saproxylics under threat at the European level is the present text. Collins & Wells (1987) include 7 saproxylic insects, among the invertebrates they list as "in need of special protection in Europe" and one outcome of their report is that *Buprestis splendens, Cerambyx cerdo, Cucujus cinnaberinus, Osmoderma eremita* and *Rosalia alpina* are now included in Appendix II of the Bern Convention, as species requiring special measures to be taken for their protection by the States which have ratified the Convention (a further saproxylic species, *Lucanus cervus*, was also added at the same time). While this clearly does not reflect the scale of the problem which exists in relation to conservation of Europe's saproxylic organisms, perhaps it will help to draw attention to the more general problem.

The objective here has been rather to provide a species list which can be used as a tool in the process of identifying forests of international importance, from either published site lists or direct site survey. There is no reason why this species list should not be expanded to embrace additional taxonomic groups. Decision as to which taxonomic groups might be added in any instance would depend upon the specialists available, as well as upon selection criteria such as those applied in this project.

5.3. Accident liability and the retention of overmature trees

In most European states the decision to retain over-mature trees or standing, dead trees, within protected areas can carry with it legal implications. These legal implications originate in the almost universal existence of the legal right to claim recompence for damage, sustained by either person or property, caused by falling trees or timber. All-too-frequently, such legal provisions are used by management authorities as an excuse for removing over-mature and dead trees (see Speight, 1973). In particular, these legal provisions are used as the basis for policy decisions to remove trees which exhibit die-back, disease, trunk cavities or significant quantities of dead wood, in locations deemed to be accessible to the general public. On sites to which members of the public have right of acces the right to claim for damages operates almost without exception. However, on land to which public access is prohibited the legal situation is more varied. In general, it can be said that it is advantageous to exclude the public from land where trees are to be allowed to live out their natural lifespan. This reduces the likelihood of accidents but, unfortunately, the general attraction that old trees have for people complicates the issue.

The problem of accident liability requires to be considered seriously by management authorities attempting to re-establish natural forest conditions. In the event that a management authority decides that it can withstand neither public criticism caused by attempting to prohibit access to woodland nor legal costs resulting from damages claims it is the rarest component of the natural forest cycle in Europe, stands of ancient trees, that are most vulnerable to loss. And it is these ancient trees that contain the highest concentrations of saproxylic invertebrates and their habitats.

In the case of a forest of recognised importance for its old forest flora and fauna, whose proprietors were prepared to allow old and dead trees to remain in situ, one way to overcome the problem of accident liability would be for the State to take responsibility for accident indemnity, as part of any management agreement reached. An alternative mechanism would be for a national indemnity fund to be set up, to provide for payment of damages claims initiated as a consequence of damage sustained by falling timber on any forest site designated for protection of nature, whether in private or public ownership and whether managed by State or private authorities.

5.4. Firewood removal

A further difficulty encountered in attempts to retain dead wood in situ is that local people and or forest managers frequently arrogate to themselves the right, with or without legal backing, to remove dead wood from a forest as firewood. Where these rights are enshrined in law they tend to be jealously protected by the few who benefit from them. In some lowland forests, this right to remove dead wood as firewood has been the only factor which has protected a forest of international importance from felling, throughout the last two or three hundred years. Practically, if not legally, traditional practices not protected by law can be as difficult to extinguish as those that are protected by law, so that any attempt to terminate practises of removal of firewood from a forest can become a very serious undertaking. Nonetheless, before any attempt to re-establish "natural" forest conditions can hope to meet with success, this problem has to be overcome. Harding(1981) advocates the establishment of new areas of coppice woodland, so that an alternative source of supplies of firewood can be made available, in areas where the local forest has traditionally provided this resource. Current pressures to remove land from agricultural use in various parts of Europe could be expected to result in the availability of areas very appropriate for establishment of new coppice woodland.

5.5. Manicuring of forests

An obsessive concern with what has euphemistically become known as "forest hygiene" has greatly reduced the ecological interest and value of many of Europe's forests, converting them to little more than tree plantations, not worthy of the name forest. There may be some justification to the view that, for areas of ground set aside solely for the production of commercial tree crops, development of a management regime akin to that found in intensive arable farming operations must be expected. However, it is hardly possible to justify extension of this type of management into forests that are serving multiple functions (e.g. in National Parks) and impossible to defend such practises in forests set aside for purposes of conserving nature. In particular, it is questionable whether the practise of systematically clearing away all fallen trees and dead wood for the sake of "tidiness" serves any useful function in such areas. Conversely, it could validly be argued that this practise has seriously detrimental effects, in that it educates the public into an entirely erroneous view of what a forest "should" look like, reduces the volume of material available for recycling through the forest ecosystem and makes it harder for both public and manager to accept that recycling is integral to a forest's activities, and vital to its long-term health.

Whether undertaken on grounds of "danger to the public", "tidiness" or "hygiene", removal of dilapidated trees, fallen trees and dead wood has the same impact upon saproxylic organisms: it eliminates their habitats, with consequent diminution in their populations. The extreme localisation exhibited by so many European saproxylics today can be attributed largely to this cause. That is not to say that these forest management practices have only come to exert a significant effect during the latter part of the present century. They have clearly been in operation for some hundreds of years. Specific instances of their detrimental effects upon saproxylic invertebrates were noted at least as long ago as the beginning of the last century (see, for example, Matile, 1986).

There is a strong case for re-education of the public and forest managers as to the value and significance of old trees and dead wood, that goes far beyond the role of these phenomena as habitats for saproxylics. But if forest managers could be convinced to leave dead trees and timber where they fall, when their only use following extraction would be as firewood, this would be a major contribution to the conservation of Europe's saproxylic invertebrates.

A factor liable to retard progress toward gaining acceptance of the principle that dead wood should be allowed to lie where it falls, is the popular superstition that dead and moribund trees are, more than anything else, a source of unspecified pestilence which will ravage the forest if they are allowed to remain. The minority of saproxylics that can cause damage and tree death, on a scale that is of commercial significance, inevitably reinforce this view. Certain Scolytidae and the weevil Hylobius abietis are prime examples. But these organisms are already firmly established within Europe's considerable hectarage of commercial forest and their continued survival there is not dependent upon management practises, like removal of dead wood, in the much smaller number and hectarage of protected forest sites and National Parks.

The superstition that old trees represent sources of "infection" for commercial tree crops is partly based on the fallacious belief that whatever occurs in any old tree both can and will move onto any nearby commercial crop. In reality, the vast majority of primary saproxylics can only function in the tissues of a narrow range of tree species (see chapter on Role of saproxylics) and the part-decomposed wood used by secondary saproxylics is of no commercial use. In particular, the saproxylic fauna of deciduous trees includes few primary saproxylic species that function in conifers, and vice versa. Removal of a moribund old oak or beech, in case it acts as a source of "infestation" of an adjacent conifer crop is thus a waste of both time and energy.

Those components of the saproxylic complex on an old tree that are least restricted by the species of tree available are the parasites and predators of other saproxylics. These old trees are, then, more likely to carry potential predators and parasites of the pest species present in an adjacent commercial tree crop, than to carry saproxylics which will cause problems there. The literature of commercial forestry and the wood-processing industry, particularly that dealing with "pests", carries a great deal of responsibility for the perennation of myth about the role of saproxylics, a matter reviewed in part by Dachy(1982). The time is long overdue that the more realistic, and factual, approach now being adopted in some of these texts (e.g. Bevan, 1987) became the norm. All too often, both forester and carpenter are still being taught to regard nature as more to blame for the consequences of poor silvicultural practise and inept wood storage than they are themselves. Some of the saproxylic invertebrates, like Cerambyx cerdo, presented as "pests" in forestry texts, are today as likely to be found in the pages of a list of threatened species as in the wood of a tree crop.

5.6. Habitat development for saproxylic invertebrates

It is almost true to say that, wherever in Europe today a 500-year-old oak or spruce is felled, or dies, a complex of saproxylic organisms and their habitats disappear from the local environment, because such trees are now so rare and cannot be replaced - other than by waiting the 500 years required for growing others! This problem is particularly acute in the "pasture woodlands" recognised by Harding and Rose(1986) as being especially important as reservoirs of saproxylics and their habitats, in areas from which forests have largely disappeared. In these pasture woodlands only very old trees remain, surrounded by grazed grassland in which there has been no regeneration of tree species for centuries. However, there are certain site management techniques with the potential to improve the chances of survival of saproxylics. These techniques will briefly be considered here. In considering the advisability of adopting management procedures aimed at encouraging the establishment of saproxylics in a forest, distance from sites known to support a significant fauna of saproxylics should perhaps be taken into account. As noted in reviewing the post-glacial history of Europe's forest, extensive tracts of Europe would seem now to be too far removed from any site possessing a well differentiated saproxylic fauna for colonisation of appropriate habitat within them to be possible.

5.6.1. Induction of premature senility in trees

For access to the tissues of a live tree saproxylic invertebrates, and saproxylic fungi, are largely dependent upon encountering some part of the tree's surface that has sustained damage which the tree has been unable to repair. Branches which snap off under weight of snow, or in gales, patches on the trunk stripped of their bark by deer, or by lightning strike, can all leave behind quantities of dead tissue suitable for colonisation by saproxylics. There are very few saproxylic invertebrates that, on occasion, penetrate directly through healthy tissues. The few that do, such as the large longhorn beetles *Aromia moschata* and *Cerambyx cerdo* and the goat moth, *Cossus cossus*, are today none of them common, since they have, not surprisingly, provoked the forester's ire for centuries. As detailed in the Chapter on the Role of saproxylics, most of the pioneer species not dependent upon mechanically damaged surface for access points enter only dead or physiologically stressed trees.

Inevitably, as a tree ages, the quantity of dead and dying tissue it carries tends to increase, because with the passage of time a succession of incidents will occur to inflict damage. This process can be emulated, in accelerated form, by appropriately designed management programmes. To some people concerned with the conservation of European wildlife it might seem outrageous to suggest that deliberate mutilation of trees should be carried out within protected areas, as a tool of responsible management. However, in forests containing but few ancient trees, and few other trees old enough to provide habitats for saproxylics before those few ancient trees have all died, induction of premature senility in some of the younger, healthy trees is one of the few ways in which continuity in the availability of habitats for saproxylics can be assured. This approach could be expected to help in maintaining saproxylic fungi, as well as saproxylic invertebrates (see, for example, Dowding, 1970). An ancillary technique would be to re-establish populations of species like Cerambyx cerdo, which can colonise healthy timber, thus themselves initiating habitat-formation for other saproxylics. Similarly, the possibility of inoculating trees with saproxylic fungi should be considered, as a method of accelerating the onset of tree senility. Since various of these fungi are evidently now becoming scarce themselves, this could also be employed as a means of securing their survival.

Today, in every part of Europe, alien (i.e. not indigenous to that part of Europe) tree species can be found, having been introduced by man. Among these introduced trees are many indigenous to other parts of Europe. For instance, European fir (Abies) and spruce (Picea) species have been introduced to many parts of Europe outside their natural range, as have chestnut (Castanea) and sycamore (Acer pseudoplatanus). In forests set aside for conservation of nature such introduced trees are frequently regarded as weed species, to be progressively eradicated. However, these trees have the potential to perform a very specific role in the present context. Because they are unwanted there is little objection to mutilating them, yet, being European in origin, they can frequently represent acceptable alternatives to trees indigenous locally, as habitats for the saproxylics indigenous to a site. Thus selective mutilation of introduced sycamore or chestnut, where they occur in a native Quercus forest, can help (see Speight, 1987) to ensure the survival of part of the saproxylic fauna associated with oak(Quercus). Similarly, selective mutilation of fir or spruce, introduced to a natural Pinus forest, could help to ensure the survival of components of the local saproxylic fauna of the pine.

Cutting off a large branch close to the trunk (particularly if a jagged cut can be achieved), or shearing away an area of bark from the trunk of a tree, are both methods of providing access for saproxylics which do not lead to immediate tree death. Ring-barking a major branch, or pollarding, can be equally effective. These techniques have the advantage that they are simple and inexpensive. There is need for some experimental carving of trunk hollows, to establish whether such sites can trigger colonisation by rot-hole faunas, since rot-holes are particularly rare other than in old, living, trees and because so many of the rot-hole saproxylics appear to be seriously under threat in Europe. Selection of trees to be used for encouragement of the saproxylic fauna and flora should depend not only upon species and size of tree, but also upon their location within the forest. Trees deep within closed canopy woodland are unlikely to be colonised as effectively as those close to flight lines like tracks, or breaks in the tree cover like natural clearings, due to concentration of the adults of so many saproxylic insects within open areas for purposes of feeding at flowers. Similarly, as Stubbs(1972) and other authors have observed, entirely exposed trees are subject to desiccation of their wood and marked temperature fluctuation in their wood, which inhibits development of a saproxylic community there.

5.6.2. Increasing the availability of dead wood

Fallen or standing dead trees(i.e. timber) represent habitats for a succession of saproxylics, as they take the process of wood decomposition towards completion. Admittedly, this phase of final recycling of a tree's substance characteristically takes no more than 25 years (except at high altitudes or at the Northern limits of forest range, where decomposition is slower), and the decaying timber is likely to provide appropriate conditions for any given species of saproxylic for only part of that 25 year period. But timber nonetheless represents a reservoir of habitats for saproxylics which can help to maintain populations of many of them at times when over-mature and senescent trees are scarce. And, unlike a 500-year-old living tree, dead wood can easily be transported to sites where it is needed. Equally, supplies of dead wood can be augmented by felling trees and leaving them to lie where they fall. Non-native trees present in a forest can be selectively felled to serve this purpose, with minimal effect on attempts to re-establish natural forest conditions.

There are three aspects of the problem of maintaining a continuous supply of dead wood in a forest that are worthy of attention. Firstly, there is the matter of ensuring that dead wood generated by a forest remains in situ. This is largely a question of ending practises of removing standing and fallen timber for reasons of public safety, firewood supply, forest hygiene and tidiness. As such, it has largely been dealt with above. Secondly, there is the problem of minimising disturbance of timber which has been left in a forest and thirdly there is the question of trucking-in dead wood to augment supplies already available.

In situations where it is not possible to ensure that old and dead trees can remain in situ throughout a forest, it can nonetheless be practicable to modify existing management so that away from public paths, in patches of forest of low productivity or difficult of access, such as in remote valleys, on steep slopes, in poorly drained hollows etc., fallen timber and old trees are deliberately left undisturbed. Introduction of such a regime could simplify forest management, as well as providing a significant contribution to conservation of saproxylic organisms.

Disturbance of fallen timber, particularly in an advanced state of decay, can be expected to accompany use of woodland by the public, unless steps are taken either to keep people away from areas with old trees and dead wood, or to explain why fallen timber should not be disturbed. But the most intensive destruction of dead wood habitats can be carried out by insect collectors and other naturalists determined to find the very organisms the wood has been left to support. This problem has been alluded to by Speight(1973) and Ehnstrom & Walden(1986). At present, there are no really adequate penalties enshrined in national nature conservation laws that might inhibit such selfish destruction, and attention might usefully be turned to this topic when by-laws are being drawn up for particular nature reserves.

Clearly, it could be a largely pointless exercise to undertake trucking-in of timber to a forest from which significant quantities of dead wood are still being removed for firewood. However, where firewood collection is a casual activity not carried out by organised groups armed with chainsaws and trailers , introduction of large-diameter logs, in lengths greater than can be fitted comfortably into the boot of a car, can be expected to result in a net increase in the volume of dead wood present on the forest floor. Units of timber of large volume can also be recognised as being of greater value to the objective of maintaining populations of saproxylics, since a large unit will take longer to decay and thus require to be replaced less frequently. Similarly, fresh-cut lengths still with the bark attached are likely to provide habitats for saproxylics for the longest periods of time, and so represent a more useful addition than debarked timber which has been cut for some years. But even the dumping of heaps of bark shavings and saw-dust onto selected sites within protected forests would help to provide habitats for some saproxylics (see Fager, 1968).

Few European forests can be said to contain adequate quantities of dead wood on the forest floor. Trucking-in of timber could thus usually be expected to result in significant increases in the populations of saproxylic organisms, both plant and animal. In the countryside at large trees are being felled all the time, for multitudinous reasons. Not infrequently they are felled with little thought as to the fate of the resulting timber. which may simply lie at the edge of a field, slowly rotting, for years. Such timber could dramatically increase the supply of dead wood in protected forests, if a concerted effort were made to obtain it.

It was noted earlier in this account that the fauna of fallen, dead trees tends to be significantly different from that of standing dead trees. This being so, in any large scale programme to bring timber into a forest, the possibility should be considered of attempting to place some of the imported trunks in holes in the ground so that they may stand vertically, to emulate the naturally occurring chandelle. An alternative would be to ring-bark some standing, live trees, an approach advocated by Cosijn(1983). Choice of locations within a forest for either introduction of additional dead wood, or ring-barking and felling, for purposes of encouraging saproxylics, should involve consideration of the same site factors as were mentioned earlier, when considering induction of senility in trees.

5.6.3. Burnt wood

Until well into the historic period, Europe's conifer forests, in particular, were repeatedly ravaged by forest fires. Increasingly effective forest protection measures have made these fires largely a thing of the past, except perhaps in the Mediterranean region. There are many saproxylics which have evolved to occupy burnt wood habitats (see text on habitats) and which do not survive in an absence of burnt timber. Today, these burnt wood saproxylics can be identified as a particular sub-set of Europe's forest fauna which is seriously threatened with extinction, en bloc, in the continent (see, for example, Heliovaarna & Vaisanen, 1983).

There has been repeated advocacy of controlled burning of limited areas of forest as a technique of forest management for nature conservation. Without some steps being taken to increase the availability of areas of burnt timber on appropriate sites it would seem unlikely that Europe's burnt wood saproxylics will survive.

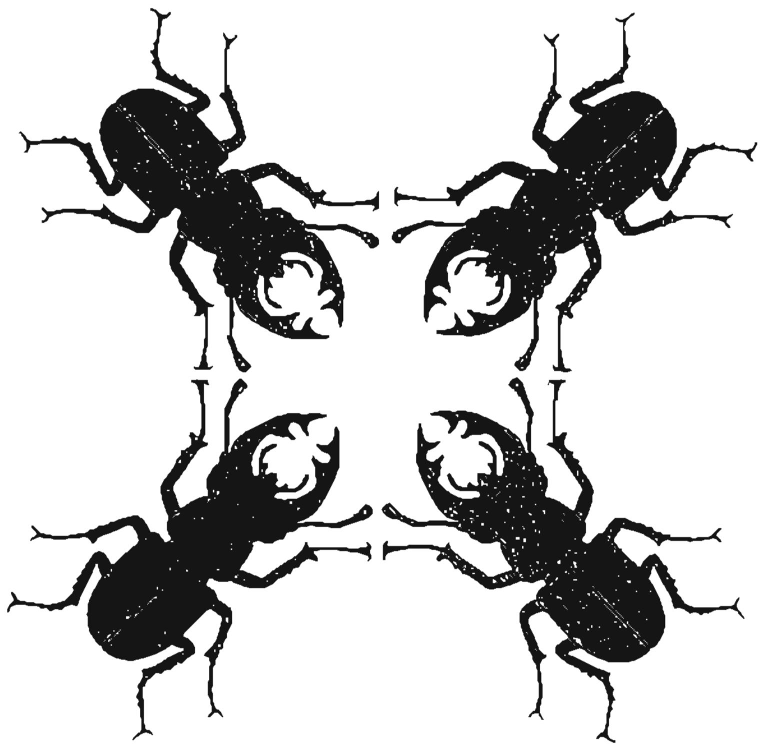
5.7. Re-establishment of species

If attempts have been made to re-establish saproxylic species in parts of their range from which they are believed to have disappeared, these efforts have gone unrecorded in the literature. At present, the comparative unpopularity of autecological studies would make attempts at re-establishment un-necessarily difficult, since, for many saproxylics, the autecological information likely to be needed in any re-establishment project is incomplete and there is little hope of current research filling the gaps. There tends to be more information available for species which have, at some time or other, been regarded as of importance in either commercial forestry or the wood-processing industry, than for species that are entirely inoffensive (see Dajoz, 1980). The inclusion of so many saproxylics on national lists of threatened species (see, for instance Gepp, 1983, Andersson et al, 1987)) provides a basis for choice of these species as research topics in various European States. Hopefully, those lists, plus the species list incorporated into the present account and the list of invertebrates added to the appendices of the Bern Convention, will focus attention upon our need for autecological data pertaining to the listed species.

For insect species with larvae that inhabit dead wood, and probably for other saproxylics as well, one technique that bears consideration in re-establishment attempts is transfer of timber known to contain populations of the developmental stages of the target organisms. In the case of insects, most pass some season of the year(usually the Winter) in a resting phase, after which the next generation of adults emerges. During the resting phase a tree containing the developmental stages of such insects could be transferred to a new site with minimal prejudice to most of them. The adults would then emerge on the new site. It is also possible to introduce suitable timber to a site known to contain populations of a target species, with the intention of subsequently transferring that timber to a site upon which it is hoped to re-establish the target organism. This approach might be expected to achieve success most easily when the target species are primary saproxylics that colonise the wood of healthy trees recently brought down by storms etc., because freshly felled trunks provided in the appropriate season can be expected to attract the adults of these species immediately and it is thus easy to ascertain that populations of the target organisms are establishing in the timber provided. The large, slow-moving, flightless, longhorn beetle Morimus asper is an example of the sort of animal which might be simple to re-establish in this fashion.

5.8. The last line of defence

Despite the best efforts of conservationists, irreplaceable stands of aged trees are still being felled in Europe, either to make way for something else or simply because they are regarded as being a danger to the public. The wood of these trees is well nigh useless for anything but firewood. In circumstances where the felling of such trees has become inevitable their value to nature conservation need not be entirely lost. If transport of the felled trees to some protected forest can be arranged and felling can be scheduled to occur during the resting phase of saproxylics likely to be found in them, there is at least the chance that some part of the saproxylic flora and fauna of these trees will be able to establish itself on the new site.



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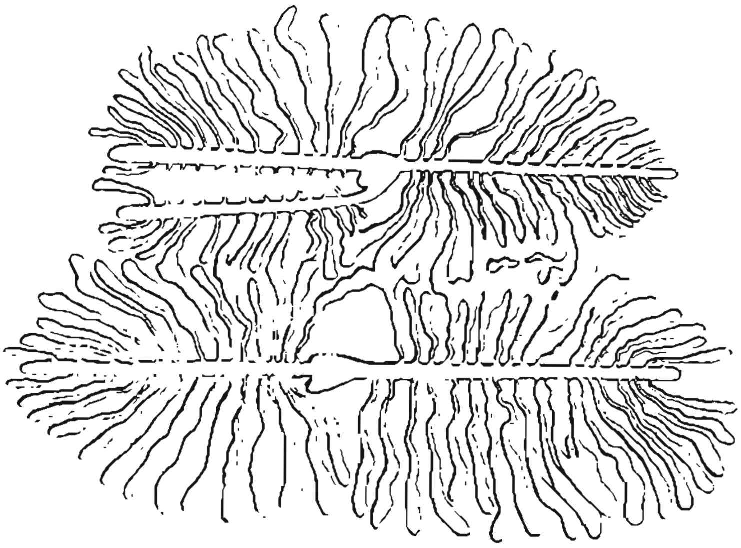

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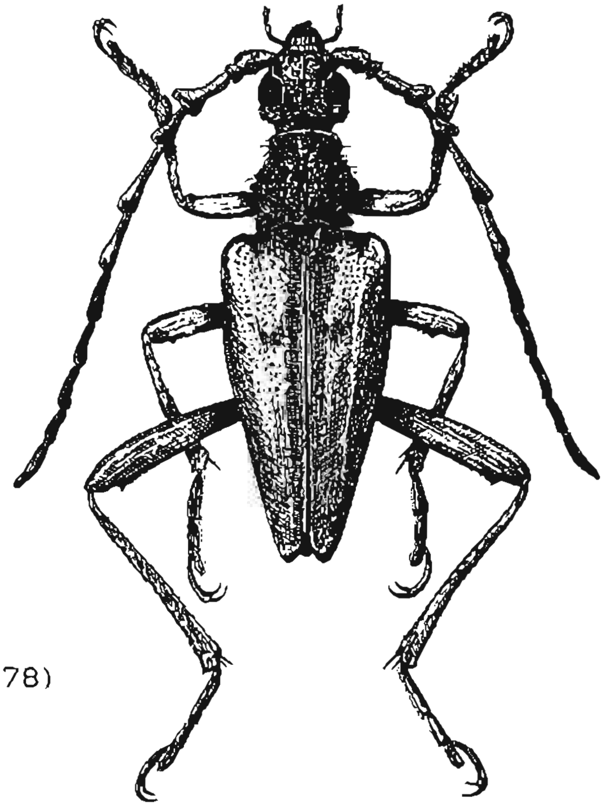


Akimerus schaefferi (after/après Villiers, 1978)

APPENDIX 1: Saproxylic insect species useful in identifying forests of international importance to nature conservation

NOTE

The 200 or so species listed below have been selected using the criteria given in Chapter 1 of this report. There are others equally suitable for inclusion, belonging to taxonomic groups not mentioned below (see Chapter 5, section 5.2.). The species used in any given instance of site assessment will, in large measure, depend upon the specialist assistance available. The taxonomic groups contributing most of the species listed below are included because of the probability that specialists in these groups would generally be available.

COLEOPTERA

Boridae: Boros schneideri (Panzer)

Buprestidae: Acmaeodera degener (Scopoli); A.revelierei Mulsant; A.tassii Schaefer; Agrilus ater (L.); A.beauprei Thery; A.convexicollis Redtenbacher; A.curtulus Mulsant & Rey.); A.grandiceps Kiesenwetter; A.guerini Lacordaire; A.hastulifer Ratzeburg; A.massanensis Schaefer; A.mendax Mannerheim; A.perisi Cobos; A.pseudocyaneus Kiesenwetter; Anthaxia bicolor Faldermann; A.castilliana Obenberger; A.ceballosi Escalera; A.espanoli Cobos; A.midas Kiesenwetter; A.segurensis Obenberger; Buprestis flavoangulata (Faimaire); B.octoguttata L.; B.sanguinea Fab.; B.splendens L.; Chalcophora intermedia (Rey); C.mariana (L.); Dicerca acuminata (Pallas); D.aenea (L.); D.alni (Fischer de Waldheim); D.berolinensis (Herbst); D.herbsti Kiesenwetter; D.moesta (Fabricius); Eurythrea austriaca (L.); E.quercus (Herbst); Kisanthobia ariasi (Robert); Latipalpis plana (Olivier); Ovalisia solieri (Castelnau & Gory); Phaenops formaneki Jakobson; P.knoteki Reiter; P.sumptuosa (Abeille de Perrin)

Carabidae: Carabus auronitens L.; C.intricatus L.

Cerambycidae: Acanthocinus reticulatus (Razoumowsky); A.henschi Reitter; A.xanthoneurus Mulsant; Acanthoderes clavipes (Schrank); Aegosoma scabricorne (Scopoli); Akimerus schaefferi (Laicharting); Anaera similis (Laicharting); Anisorus quercus (Goetz); Anoplodera sexguttata (Fabricius); Brachyleptura strangulata (Germar); Callimellum abdominale (Olivier); Cerambyx cerdo L.; Chlorophorus herbsti (Brahm); C.hungaricus Seidl.; Cornumutila quadrivittata (Gebler); Cortodera aspromontana G.Muller; Cyrtoclytus capra (Germar); Glaphyra marmottani (Brisout); Hesperophanes pallidus (Olivier); Icosium tomentosum Lucas; Lamia textor (L.); Leioderus kollari Redtenbacher; Leiopus punctulatus (Paykull); Leptura arcuata Panzer; L.aurulenta Fabricius; L.scutellata (Fabricius); Mesosa curculionoides (L.); M.myops (Dalman); Monochamus urussovi (Fischer v. Waldheim); Morimus funereus Mulsant; Necydalis major L.; N.ulmi Chevrolat; Notorrhina punctata (Fabricius); Nustera distigma (Charpentier); Oxymirus cursor (L.); Oxypleurus nodieri Mulsant; Pogonocherus eugeniae Ganglebauer; Prinobius scutellaris (Germar); Rhamnusium bicolor (Schrank); Rhopalopus femoratus (L.); R.insubricus (Germar); R.macropus (Germar); R.ungaricus Herbst; Saperda perforata (Pallas); Saphanus piceus (Laicharting); Tragosoma depsarium (L.); Tetrops starki Chevrolat

Cetoniidae: Cetonischema aeruginosa (Drury); Eupotosia koenigi (Reitter); Gnorimus decempunctatus Helf.; G.octopunctatus (Fabricius); Liocola lugubris (Herbst); Osmoderma eremita (Scopoli); Trichius sexualis Bedel

Cucujidae: Cucujus cinnaberinus (Scopoli); Laemophloeus corticinus Erichson; Notolaemus castaneus (Erichson); Prostomis mandibularis Fabricius

Elateridae: Ampedus cardinalis Schiodte; A.elegantulus Schonherr; A.fontisbellaquei Iablokoff; A.hjorti Rye; A.megerlei (Lacordaire); A.nigerrimus (Lacordaire); A.quadrisignatus (Gyllenhal); A.ruficeps (Mulsant et Guillebeau); Anchastus acuticornis (Germar); Anostirus parumcostatus (du Buysson); Athous mutilatus Rosenhauer; Cardiophorus anticus Erichson; C. gramineus (Scopoli); Denticollis rubens Piller & Mitterpacher; Elater ferrugineus L.; Ischnodes sanguinicollis Panzer; Lacon fasciatus (L.); L.lepidopterus (Panzer); L.querceus (Herbst); Limoniscus violaceus (Muller); Megapenthes lugens (Redtenbacher); Orthitales serraticornis (Paykull); Porthmidius austriacus (Schrank)

Lucanidae: Aesalus scarabaeoides (Panzer); Ceruchus chrysomelinus (Hochenwarth); Dorcus musimon Gene; Pseudolucanus barbarossa Fabricius

Oedemeridae: Ditylus laevis (Fabricius); Ischnomera cyanea (Fabricius)

Peltidae: Grynocharis oblonga (L.); Peltis grossa (L.);

Pythidae: Pytho abieticola Sahlberg; P. depressus (L.); P.kolwensis C.R.Sahlberg

Rhysodidae: Clinidium canaliculatum Costa; Rhysodes germari Ganglebauer; R. sulcatus (Fabricius)

DIPTERA

Canthyloscelidae: Hyperoscelis eximia (Boheman)

Coenomyiidae: Coenomyia ferruginea (Scopoli)

Keroplatidae: Keroplatus tipuloides Bosc

Pachyneuridae: Pachyneura fasciata Zetterstedt

Stratiomyiidae: Berkshiria hungarica (Kertesz); Odontomyia annulata (Meigen); Clitellaria ephippium (Fabricius)

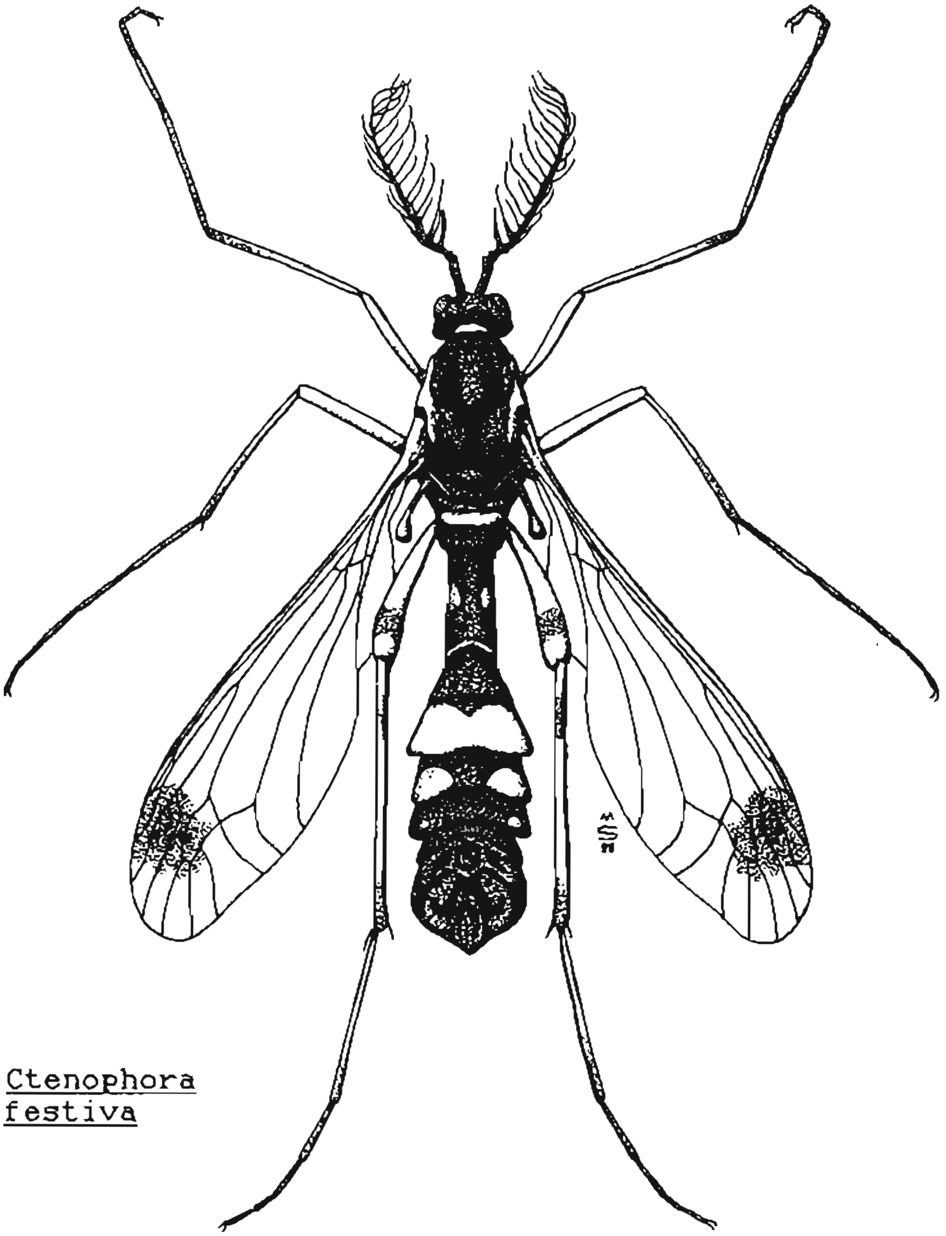
Syrphidae: Brachyopa bicolor (Fallen); B.ferruginea (Fallen); B.panzeri Goffe; B.vittata Zetterstedt; Brachypalpus chrysites Egger; B.valgus (Panzer); Caliprobola speciosa (Rossi); Callicera aenea (Fabricius); C.aurata (Rossi); C.loewi Verrall in Collin; C.macquarti Rondani; C.rufa Schummel; C.spinolae Rondani; Ceriana conopoides (L.); Chalcosyrphus eunotus (Loew); C.femoratus (L.); C.jakobsoni (Stackelberg); C.pigra (Fabricius); C.valgus (Gmelin); Criorhina pachymera Egger; Doros destillatorius Mik; Ferdinandea aurea Rondani; F.ruficornis (Fabricius); Lejota ruficornis (Zetterstedt); Mallota dusmeti Andreu; M.fuciformis (Fabricius); M.megilliformis (Fallen); Milesia crabroniformis (Fabricius); M.semiluctifera (Villeneuve); Myolepta difformis Czerny & Strobl; M.helvetica (Wainwright); M.nigritarsis Coe; M.obscura Becher; M.potens (Harris); M.vara (Panzer); Pocota personata (Harris); Psarus abdominalis (Fabricius); Psilota anthracina Meigen; Sphecomyia vespiformis Gorski; Sphiximorpha subsessilis (Illiger in Rossi); Spilomyia boschmai Lucas; S.digitata (Rondani); S.diophthalma (L.); S.manicata (Rondani); S.saltuum (Fabricius); Temnostoma apiforme (Fabricius); Xylota fulviventris Bigot; X.meigeniana (Stackelberg); X.suecica (Ringdahl)

Tipulidae: Ctenophora elegans (Meigen); C. festiva Meigen;

C.flaveolata (Fabricius); C.guttata Meigen; C.ornata Meigen; Tanyptera nigricornis (Meigen)
Xylomyiidae: Solva interrupta Pleske; S.maculata (Meigen)

HEMIPTERA
Aradidae: Aradus angularis J.Sahlberg; A.anisotomus Puton; A.aterrimus Fieber; A.bimaculatus Reuter; A.brevicollis Fallen; A.conspicuus Herrich-Schaeffer; A.erosus Fallen; A.laeviusculus Reuter; A.signiticornis F.Sahlberg; A.truncatus Fieber; Mezira tremulae (Germar)

HYMENOPTERA
Orussidae: Orussus abietinus (Scopoli); O.henschi Mocsary; O.unicolor Latreille
Siricidae: Tremax alchymista Mocsary; T.fuscicornis (Fabricius); T.magus (Fabricius)
Xiphydriidae: Konowia betulae Enslin; K.guntionensis Zambou; K.megapolitana Brauns; Xiphydria camelus (L.); X.longicollis (Geoffroy); X.picta Konow; X.prolongata (Geoffroy)



Ctenophora
festiva

APPENDIX 2: European forests identified as being of potential international importance by their fauna of saproxylic invertebrates

Note

In the list, B/P/P/P = Betula/Picea/Pinus/Populus tremula, C/F/Q = Carpinus/Fagus/Quercus

AUSTRIA

Baden, 8 Wien (Niederösterreich): Fagus
Gams b. Heiflau (Steiermark): Fagus/Picea
Gesaeuse (Steiermark): Fagus/Picea
Geschriebenstein Mt. (Burgenland): Fagus/Quercus/Pinaceae
Gruenburg, Auwald (Oberösterreich): Fagus/Tilia/Picea etc.
Herberstein, Tierpark, Schloss Herberstein (E.Steiermark): Quercus/Castanea/Fraxinus
Hoergas, N.Graz (Steiermark): Fagus/Picea
Kaltenleutgeben (Niederösterreich): Fagus/Quercus
Lainzer Tiergarten (Wien, W.): Quercus/Fagus
Laxenburg (Niederösterreich): Quercus
Lunz am See (Niederosterreich): Picea
Moedling (Niederösterreich): Fagus etc.
Molln (Oberösterreich): Fagus/Picea
Mur-Auen, zwischen Mureck und Radkersburg (S.Styria): Quercus/Salix/Populus/Ulmus
Perchtoldsdorf (Wien/Niederösterreich): Quercus/Carpinus
Pfenningberg (Oberösterreich): mixed
Pitten (Niederösterreich): Picea
Prater, Auwaldrest (Wien 2): Populus etc.
Purkersdorf, Wien, W. (Niederösterreich): Quercus/Fagus
Reichraming (Oberösterreich): Fagus/Picea
Schneeberg (Niederösterreich): Picea/Fagus
Schoberstein, Ennstal Mt., (Oberösterreich): Fagus/Picea
Tullnerbach, Wienerwald (Niederösterreich): Fagus/Quercus
Wechselalpe Mt., (Niederösterreich): Picea

BELGIUM

Bois d'Olfagne (Tenneville), FR 75: Fagus
Bois du Chateau Brien (Lembeek), ES 81: Fagus
Hertogenwald Oriental, district 49 (Alt-hattlich), KB 90: Fagus
Nisramont (Rive droite, lac Nadrin), FR 95: Quercus/Acer/Betula
Poncelles (Titigny), FR 80: Alnus

CYPRUS

Tripylos NR, Paphos Forest: Cedrus/Pinus.

DENMARK

Bognaes Storskov (NEZ), UB 17: Fagus/Quercus
Draved Skov (SJ), MF 99: Alnus/Corylus/Quercus/Tilia
Frijsenborg, Lille Dyrehave (EJ), NH 53: Fagus/Quercus
Jaegersborg Dyrehave (NEZ), UB 48: Fagus
Jaegerspris Nordskov (NEZ), PG 80/PG 89: Alnus/Quercus
Kastrup Dyrehave (SZ), PG 63: Fagus/Quercus
Krenkerup Haveskov (LFM), PF 77: Fagus/Quercus
Maltrup Skov (LFM), PF 67: Fagus/Quercus
Nørholm skov, 32U MG77 (S Jutland): Quercus
Suserup Skov (SZ), PG 64: Fagus/Fraxinus/Quercus
Vallø Dyrehave (SZ), UB 24: Fagus

FEDERAL REPUBLIC OF GERMANY

Baumweg (27 km. S. of Oldenburg) 52 54'N, 8 9'E: C/F/Q
Ellernbusch (10 km. N. of Oldenburg) 53 14'N, 8'14 E: F/Q
Elm (20 km. S.E. of Braunschweig) 52 11'N, 10 51'E: Alnus/Fagus/Picea/Quercus
Hartz mountains (SE of Hanover): Fagus/Picea/Sorbus aucuparia
Kleiner Berg (18 km. S. of Osnabruck) 52 07'N, 8 07'E: Prunus avium
Mansholter Holz (10 km. N.W. of Oldenburg) 53 13'N, 8 06'E: Fagus/Quercus
Schönbuch, N. of Tubingen (Baden-Wurtemburg): Fagus/Quercus
Staatsforst Hasbruch (23 km. ESE of Oldenburg) 53 04'N, 8.29'E: C/F/Q
Staatsforst Neuenburg (29 km. NNW of Oldenburg) 54 24'N, 7 59'E: C/F/Q
Staatsforst Palsterkamp (12 km. S. of Osnabruck) 52 9'N, 8 06'E: Fraxinus
Urwald an der Sababurg (30 km. N. of Kassel) 51 32'30"N, 9 30' 30"E: Fagus/Quercus

FINLAND

Hirvihaaran Metsäkulma, Uudenmaan lääni, Mäntsälä: B/P/P/P
Koli, Pohjois-Karjalan lääni, Lieksa: B/P/P/P
Kolmikanta, Mikkelin lääni, Mäntyharju: B/P/P/P
Kotisten aarnialue, Hämeen lääni (EH) Laami, Evo: B/P/P/P
Oulanka, Oulun lääni (KS) Kuusamo: Picea/Pinus
Pallosenvaara, Pohjois-Karjalan lääni (PK), Ilomantsi(Lieksa): B/P/P/P
Pisavaara, Lapin lääni (PP), Rovaniemi/Tervola: Picea/Pinus
Pyhän-Hakki, Keski-Suomen lääni (PH), Saarijarvi: Picea/Pinus
Scitseminen, Hämeen lääni/Turun ja Porin lääni, Kuru/Ikaalinen: Picea/Pinus
Vesijako, Hämeen lääni (EH), Padasjoki: Picea/Pinus

FRANCE

Aitone (Corsica): Pinus spp.
Baranette, à coté du lac d' Oredon (Hautes Pyrenées): Picea/Pinus uncinata
Belésta F.de, nr.Carcassone (Aude/Ariège): Picea
Blois, F.de (Loir-et-Cher): Quercus
Born, F.d. (Dordogne): C/F/Q
Boulogne (Loir et Cher): C/F/Q
Bragues, F.de (Ariège): Pinus
Carenca, vallée de la (Pyrenées Orientales): Pinus uncinata
Carlencas, F.de (Hérault): Pinus spp.
Citeau (Bourgogne): Quercus
Compeigne (Oise): C/F/Q
Creux de l'Envers (Jura): Abies/Fagus
Fontainebleau (Seine et Marne): C/F/Q
Grésigne (Tarn): C/F/Q
Hasenlach-Kopf (S face), F Domaniale de Kruth (Haut-Rhin): Abies
Iraty (Pyrenées Atlantiques): Fagus/Abies
Loches (Indre et Loire): C/F/Q
Massane (Pyrenées Orientales): Fagus/Quercus/Acer
Montargis (Loiret): C/F/Q
Morvan, Mont de (Nièvre): Quercus
Orient (Aube): C/F/Q
Orléans (Loiret): C/F/Q

Ospédale (Corsica): Pinus spp.
Osthouse (Bas-Rhin): C/F/Q
Othe (Yonne/Aube): C/F/Q
Raismes (Valenciennes): Quercus
St.Baume (Var): C/F/Q + Taxus
St.Guilhem, F.de (Hérault): Pinus spp.
Tronçaix (Allier): C/F/Q + Pinus
Vizzarone (Corsica): Fagus

GREECE

Cephalonia Nat.Pk. (Cephalonia), slopes of Mt.Enos: Abies cephalonica.
Chelmos, Mt., at 1400-1600m (N.Pelopponese): Pinaceae
Olympos, Mt., N.E.slope at 1400-1600m: Pinus spp.
Parnassus, Mt., E.slopes at 1500-1800m: Abies alba
Taygetos Oros, E.slopes nr. Anavriti, at 1400-1600m, Peloponnesos: Pinaceae
Timfristos, Mt., E.slopes at 1500m, pass between Timfristos and Karpenision: Abies alba

ITALY

Aquasanta, Monti Sibillini (Marche): C/F/Q
Bolzano (Trentino): Quercus/Castanea/Fagus/Picea
Bosco della Fontana (Mantova): Carpinus/Quercus
Caldes, F.d., Sezioni 12-15, Valle di Sole (Sole): Picea
Lessini, F.d. Monti, Comune di Ala (Trento): Abies/Fagus/Picea
Magnifica, F.d. Comunita di Fiemme, Dist.7, Valle di Fiemme (Fiemme): Larix/Picea/Pinus cembra
Sasso Fratino, Casentinesi forests (Emilio-Romagna): Fagus/Abies
Sibilla, Monte (Marche): C/F/Q
Pieve di Denno, Sez.70 (Trento): Abies/Larix
Torrichio, Riserva naturale del Monte (Maserata): C/F/Q

LIECHTENSTEIN

Garselli-Zigerberg, Saminatal: Abies/Picea/Acer/Fagus
Poskahalde (Triesen): Quercus/Fagus/Fraxinus/Picea

NORWAY

Kragerø (Kragerø/Telemark): Betula/Quercus/Alnus
Nes, Jernverk (Tvedestrand/Aust-Agder): Betula/Quercus/Alnus
Odal, Ser-Odal, Nord-Odal (Hedmark): Pinus/Picea/Betula
Rauøy, Onsøy (Ostfold): Fraxinus/Quercus/Ulmus
Reier, Moss , NL 921-895 (Ostfold): Quercus/Tilia/Fraxinus
Risør (Risør/Aust-Agder): Quercus/Pinus/Picea

SPAIN

Cazorla y Segura, Sierra d. El Pozo (Gaérr): Pinus/Quercus
Dehasa d.l. Alfaguara, Sierra d.Maria (Almeria): Pinus/Quercus
Hayedo d.Montejo, Monteyo d.l. Sierra (Madrid): Fagus/Quercus
Iraty, bosque d' (Navarre): Picea/Fagus
Montseny, monte del (Lerida): Fagus/Abies
Pijaral, El, Tenerifé (Islas Canarias): Laurus/Ilex/Prunus/
San Privat de Bas, 600-800m ("Nr.Orlot, N.E.Spain"): Castanea
Pinar de Garafia, La Palma (Islas Canarias): Pinus canariensis
Pinar, El, Sierra de Grazalema (Cadiz): Abies pinsapo/Quercus faginea
Pinsapar, El, Sierra d.l. Nieves od. Tolox (Malaga): Abies pinsapo/Quercus/Fagus/Ilex

SWEDEN
Båtfors region (Uppland): Quercus/Populus/Picea
Birt-järnsberget (Dalarna): Picea
Bjärka Säby region (Östergötland): Quercus
Bjurkärr, 56.37'N, 13.79'E: Fagus
Blåkölen (Norrbotten): Picea
Ekön (Södermanland): Tilia
Eldgarn (Uppland): Tilia
Gotska Sandön (Gotland): Pinus
Granberget (Norrbotten): Picea
Häckeberga (Skåne): Fagus
Hallands Vadero (Skåne): Fagus
Halltopshage (Oland): Quercus
Hornsö (Småland): Fagus
Klöverträsk (Norrbotten): Populus
Krokliden, 65.52'N, 21.20'E: Pinus/Populus tremula
Kuusivaara, 66.40'N, 23.0'E: Picea
Maltesholm, 55.55'N, 13.98'E: Fagus
Muddus (Lappland): Pinus
Norra Kvill (Småland): Pinus
Örups almskog (Skåne): Ulmus
Paskatieva, 66.40'N, 22.30'E: Pinus
Reivo, 65.47'N, 19.0'E: Pinus
Skäralid (Skåne): Fagus
Spjutoerget, 65.30'N, 20.3'E: Pinus
Strömserum (Småland): Quercus
Strömsholm (Västmanland): Quercus/Ulmus
Tinäset, 60.12'N, 16.43'E: Populus
Tromtö, 56.10'N, 16.38'E: Fagus
Vändåtberget, 63.58'N, 18.18'E: Picea
Värlebo, 57.03'N, 16.53'E: Fagus
Värnanäs, 56.30'N, 16.08'E: Fagus

SWITZERLAND
Aletschwald, 2000m (Valais): Pinus
Bois de Chênes, Ferreyres-la-Sarraz (Vaud): Quercus/Buxus
Bois de Finges/Pfynnwald, Communes Scerres (Valais): Pinus/Betula
Derborence (Valais): Picea/Pinus
Parc Nation Suisse (Graubünden): Pinus spp.

UNITED KINGDOM
Abernethy (Inverness): Pinus
Epping (Essex): C/F/Q
Moccas Pk. (Hereford/Worcester: Fagus/Quercus
New Forest (Hampshire): Fagus/Quercus
Windsor Forest/Windsor Gt.Pk. (Berkshire): Fagus/Quercus

APPENDIX 3 Recommendation of the Committee of Ministers on the protection of saproxylic organisms and their biotopes

The specialist recommendations produced as an integral part of this report have since been debated by the relevant committees of the Council of Europe and, in duly revised format, approved and issued by the Committee of Ministers. Only one of the recommendations failed to reach the final document, namely that judicious use of controlled burning should be recognised as an appropriate management tool in forests known to possess burnt-wood saproxylics (one of the most threatened groups of forest organisms in Europe). In the format agreed by the Committee of Ministers, the recommendations have now been published as Recommendation R"88"10. This is reproduced in full below. Agencies responsible for nature conservation in Member States have now been made aware of the existence of this Recommendation. Individuals and organisations concerned for the conservation of the flora and fauna of ancient European forests should also be aware of this Recommendation, in case there is a need to remind conservation agencies and forest managers of its provisions.

COUNCIL OF EUROPE
COMMITTEE OF MINISTERS

RECOMMENDATION No. R"88"10
OF THE COMMITTEE OF MINISTERS TO MEMBER STATES

ON THE PROTECTION OF SAPROXYLIC ORGANISMS AND THEIR BIOTOPES

(adopted by the Committee of Ministers, 13 June 1988,
at the 418th meeting of the Ministers' Deputies)

The Committee of Ministers, under the terms of article 15.b of the Statute of the Council of Europe,

Having regard to the Convention on the Conservation of European Wildlife and Natural Habitats of 19 September 1979 which lists a number of saproxylic insects, and in particular to article 4 thereof on the protection of habitats;

Having regard to its Resolution (76) 17 on the European network of biogenetic reserves, as well as to its Recommendation R (86) 10 concerning the Charter on Invertebrates;

Referring to its Recommendation on ancient natural and semi-natural woodlands;

Referring to the study on saproxylic invertebrates and their conservation commissioned by the European Committee for the conservation of wildlife and natural resources and published in the Nature and Environment series;

Considering that the diversity of wildlife is essential to the maintenance of the biological balance of ecosystems and that here invertebrates play a determinant part which is often under-estimated and requires thorough study;

Recognising that saproxylic organisms are a fundamental part of the European natural heritage for their scientific, educational, cultural, recreational, aesthetic and intrinsic value;

Noticing that in Europe a large number of saproxylic organisms have become extinct and that many others risk becoming so if their decline continues;

Noting that the alarming situation of saproxylic organisms is attributable primarily to the loss or deterioration of their habitat, in particular as a result of the disappearance or intensive exploitation of natural forests;

Considering that saproxylic organisms are excellent bioindicators of the natural conditions of the most interesting and most characteristic European forests:

RECOMMENDS THE GOVERNMENTS OF THE MEMBER STATES OF THE COUNCIL OF EUROPE TO:

1. give particular consideration to forests known to possess a well-differentiated fauna or flora of saproxylic organisms when deciding protection priorities in natural woodlands;

2. bearing in mind their essential role for the conservation of saproxylic organisms, protect all ancient natural forests;

3. consider survey of saproxylic organisms in assessing the quality of forests for nature conservation purposes, particularly where the intention is to re-establish natural forest conditions within a protected area:

4. manage protected forests according to local conditions and in such a way as to maintain their saproxylic fauna and flora, for instance by

   - avoidance of the removal of firewood, fallen timber and dead trees wherever possible;

   - avoidance of undue human interference in protected natural and ancient forests which are important for the conservation of saproxylic invertebrates;

   - enlargement of the protected area when it contains only small enclaves of ancient trees;

   - delimitation of adequate areas where wood and fallen trees can be left untouched in forests where these practices may not seem desirable for the whole forest;

5. appeal to the cooperation and skills of forest managers; provide them with information on the positive role of saproxylic organisms in forest dynamics and to the consideration of old trees and dead wood as important elements within the forest ecosystem rather than sources of disease, particularly in cases where the old trees are deciduous species within commercial conifer forest or vice

versa;

6. take steps to encourage the in-depth study of the ecology of poorly known threatened saproxylic species, so that further management practices appropriate for promoting the survival of these species can be identified;

7. take steps to re-establish threatened saproxylic species in parts of Europe from which they have disappeared;

8. encourage and promote education of the public visiting forests in the interest of saproxylic organisms and the importance of not disturbing fallen timber or dead trees;

9. consider, for integration in the European network of biogenetic reserves, the forests mentioned in the above-mentioned study, in view of their potential international importance because of the saproxylic organisms which they shelter;

10. ensure, in States where the maintenance of moribund and dead trees would be in conflict with legal requirements for access to land by the public, that selected sites can be exempted from such legal requirements, so that trees can be allowed to die naturally of old age.

Compilers' note: Pages 10, 44, 58, 68, 72, and 80 were blank.

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