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PREFACE

The present volume completes the first five years of life for the *Annual Review of Entomology*. (Although this is only Volume 4, a year of exploration and preparation preceded Volume 1.) During this formative period much has occurred; the *Review* appears to have passed through its "baptism of fire," and, we trust, has taken its place throughout the world as an accepted and stabilized publication in entomology. This accomplishment could not, of course, have been made without the support of many individuals (especially subscribers) and some organizations. In the latter category are the publisher, Annual Reviews, Inc., its Managing Editor, Dr. J. Murray Luck, and the Entomological Society of America.

Although your Editor had been agitating for some type of review publication in entomology since 1945, it was the Society which, through its officers, first gave substance to his hope that such a publication were possible. A general account of the genesis and organizational arrangements pertaining to the *Review* may be found in the *Bulletin of the Entomological Society of America* (Vol. 1, No. 2, 1955). But some of the more intimate details of the *Review's* beginnings are not included in that account. As we glance back, we are again reminded of the great credit that must be extended to men like Charles E. Palm, who, as President of the Society, gave an attentive ear to pleas that the Society take the lead in doing something about the matter. In 1953 he appointed a committee to examine the problem of providing adequate reviews of entomological literature. After a period of arduous work, study, and thorough analysis, the committee recommended that a review publication of the type published by the nonprofit organization Annual Reviews, Inc., would best answer the needs for entomology from an over-all viewpoint. Nor can we forget the interest and support of E. Gorton Linsley, who accompanied the Editor to a crucial meeting with officers of Annual Reviews, Inc., and who, along with others, gave his support to the *Review* when it was being considered by the Society's Governing Board.

From this distance it might appear that it was a logical thing for the Society to give its encouragement and support to the undertaking. It should be remembered, however, that consideration of this matter came at a time when the Society had just completed consolidation, and the demands on the Society's finances were at a peak. Nevertheless, because of the courage, understanding, and farsightedness of the members of this Governing Board and the officers of the Society, the critical decision was made to give the *Review* its moral and financial support according to the terms outlined in the *Bulletin* article to which we have already referred.

As previously agreed, with the completion of the present volume the financial obligations (largely recompensed) of the Society to the *Review* come to an end. Henceforth, Annual Reviews, Inc., will assume this responsi-

bility in full, depending, of course, upon the continued and increasing support (through individual subscriptions) of entomologists everywhere. Especially will the *Review* require the continued support of Society members, who constitute the core of American entomologists. In this connection, it is important to remember that the Society will continue to receive a discount on the retail price of all subscriptions submitted by the Society on behalf of its members. Accordingly, members desiring to benefit the Society while at the same time availing themselves of the *Review* (at the same price) thus have an opportunity to do so. It is appropriate here that all of us directly associated with the *Review* not only register again our thanks and appreciation to the Society for its past enthusiastic and generous support, but also record and acknowledge the fact that without this support the *Review*, once initiated, might never have been able to acquire the use of its wings to soar independently among the best of biological publications.

While it is customary to acknowledge the aid and service of our Editorial Assistant, in the present case this is no mere ritualistic performance. Mrs. Margaret M. Janofsky has not only immensely lightened our editorial load, but has, with outstanding efficiency and effectiveness, handled many of the important details that are associated with the editing and publishing of a first-rate volume.

R.G.	C.B.P.
R.L.M.	R.F.S.
C.D.M.	E.A.S.
C.M.W.	

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ECOLOGY OF CERAMBYCIDAE¹

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INTRODUCTION

The object of this review is to bring together available information on the environmental relationships of Cerambycidae, including physiological and ethological features which may have influenced their evolution and survival. Except for larval food and nutrition, which influence host specificity, emphasis has been placed upon adult ecology, since larval habits have been summarized by Kemner (168), Craighead (77), Kojima (175), Beeson & Bhatia (21), Duffy (93, 94), and others. Although nearly 1000 sources have been consulted, it has been possible to cite less than one-third of these. In selecting items for inclusion, I have tried to emphasize the more recent or the more comprehensive of alternative references, with special consideration to those which include bibliographies. No serious attempt has been made to develop the various facets of the subject historically.

SIZE AND SCOPE OF FAMILY

The family Cerambycidae comprises a group of phytophagous Coleoptera, the adults of which are commonly referred to as long-horned or longicorn beetles, the larvae as round-headed borers. Seven subfamilies are currently recognized and approximately 20,000 species have been described, although the most recent world catalogue (the parts of which are from 35 to 45 years out of date), lists only about 14,000 (Table I). Most of the genera in the larger subfamilies are small, with an average ranging from about 4 to 6.5 species per genus. One of the largest is the lamiine genus *Glenea* with nearly 600 currently recognized species in Tropical Africa, South and East Asia, and the South Pacific region (38). At the other extreme are the more than 1000 monotypic genera (Table I).

GEOGRAPHICAL DISTRIBUTION

The zoogeography of animals other than insects has been recently reviewed by Darlington (82), that of insects by Gressitt (135). The ecological aspects of the subject have been emphasized by Uvarov (314), Lindroth (200, 201), and others. Although, broadly speaking, climatic factors and availability of suitable food plants are the main factors governing the distribution of Cerambycidae in the world today [Linsley (206, 209)], past cli-

¹The survey of literature pertaining to this review was completed in May 1958. The significant paper by W. Funk—"Zur Biologie und Ethologie einheimischer Lamiinen" (*Zool. Jahrb. Abt. Systematik Ökol. u. Geograph. Tiere*, **85**, 73-176, 1957)—was not available in time for consideration.

TABLE I
DISTRIBUTION OF GENERA AND SPECIES AMONG THE
VARIOUS SUBFAMILIES OF THE CERAMBYCIDAE*

Subfamily	Number of Species	Number of Genera	Mono-typic Genera	Per Cent Mono-typic	Genera with 50+ Species	Species in Largest Genus	Average Number of Species per Genus
Lamiinae	7665	1167	503	43	22	323	6.6
Cerambycinae	4773	874	394	45	11	104	5.5
Lepturinae	799	124	62	50	1	125	6.4
Prioninae	589	109	45	41	1	53	5.4
Aseminae	54	13	8	61	0	18	4.1
Spondyliinae	4	2	1	50	0	3	2.0
Parandrinae	31	2	1	50	0	30	15.5
Family	13,915	2291	1014	44	35	323	6.1

* Data compiled from Aurivillius (7) and Lameere (178)

mates, and the evolution and spread of past floras have had a profound influence on the distributional and evolutionary history of the surviving, present-day representatives of the family (214). Thus, for example, the early holarctic elements of the cerambycid fauna of the Northern Hemisphere were largely associated with the Arcto-Tertiary flora (8), which moved southward during the Tertiary period and replaced pre-existing tropical floras of the Cretaceous period. These early northern types are now represented discontinuously in Europe, Eastern Asia (Japano-Manchurian), Western North America (Vancouveran), Eastern North America (Alleghenian), and on the Mexican Plateau (206). Included are such genera as *Spondylis*, *Rhopalopus*, *Clytoleptus*, *Cortodera*, *Ergates*, *Rosalia*, *Atimia*, *Callimoxys*, *Gaurotes*, *Plectrura*. At least nine of these are represented in the Oligocene beds of Florissant, Colorado, by forms closely related to living species in these widely separated areas (209).

In those cerambycid groups of which the morphological relationships are sufficiently understood to permit of phylogenetic interpretation, their major patterns of distribution can readily be explained in terms of the present arrangement of the world land masses (206). The temperate fauna of the Northern Hemisphere has a large number of elements in common (Table II) which presumably were derived from relationships extending back into the Cretaceous and early Tertiary periods (133, 206, 214). At present, the distributions of these elements and of the woody plants which serve them as hosts are widely discontinuous, these discontinuities apparently reflecting segregation in the face of gradual climatic changes during the Tertiary and centers of survival during the extremes of the Cenozoic. Overlying these dis-

continuous patterns are broad Holarctic circumpolar ranges of genera and some species which apparently reflect postglacial dispersal. The vast tropical belt is extremely rich in Cerambycidae (7, 25), and although many tribes are essentially pantropical in range, this is true of relatively few genera and no species (beyond those dispersed by man) [Linsley (212)]. Thus, the tropical faunas of the Eastern and Western hemispheres appear to have been separated for long periods of time. At present they are represented in residual pockets and encroachments to the north and south of the tropics proper, especially in southeastern Asia (21) and southeastern United States (206). In North America the tropics have contributed heavily to the derived fauna of the Sonoran Desert, but apparently this has not been true of the Sahara Desert of Africa (269, 316). South temperate Cerambycidae, although having a few elements in common suggesting phylogenetic affinity, especially at the tribal level (113), generally have their own characteristics on the various continents (32, 155, 227, 260), and the faunas of intercontinental Southern Hemisphere plants appear to have been independently derived wherever they occur. Thus, the discontinuities in Southern Hemisphere distribution apparently have not resulted from contiguity of geographical origin. Several north-south, transtropical distributions are evident in both the Old and New World, but generally the Southern Hemisphere elements are so isolated morphologically as to suggest that the geographic relationship is an ancient one. Some of these may be more recent, as the similarity of certain elements in the desert faunas of western North and South America, but they need further study and analysis.

TABLE II

CONTEMPORARY GEOGRAPHICAL RANGES OF NORTH AMERICAN CERAMBYCIDAE*

	Genera		Species	
	Number	Per Cent	Number	Per Cent
World Wide	4	1.70	0	0
Holarctic	34	14.47	9	1.03
Nearctic	10	4.26	14	1.60
Alleghenian	30	12.76	264	30.28
Vancouverian	16	6.81	147	16.86
Rocky Mountain	2	0.85	39	4.47
Great Basin	0	0	27	3.09
Californian	18	7.66	45	5.16
Sonoran	44	18.72	194	22.25
Eastern Austral	10	4.26	0	0
Austro-Riparian	0	0	46	5.28
Neotropical	67	28.51	87	9.98
Totals	235	100	872	100

* After Linsley (214)

The Oriental and Papuan (New Guinea) faunas are very rich in Cerambycidae. In India alone, about 1200 species are known, more than 700 of which are Lamiinae (21), although these figures include some Palearctic elements in the Himalaya and higher mountains to the north. Gressitt (*in litt.*) has on hand an estimated 1000 species from the New Guinea-Solomon Island region, the Lamiinae far outnumbering the Cerambycinae. New Guinea has one lepturine, the Solomons none.

Australia has about 1000 known species of Cerambycidae in less than 275 genera (227). Only four subfamilies are represented, the Prioninae, Parandrinae, Cerambycinae and Lamiinae, and certain groups of Cerambycinae are lacking. Even so, Australia is also the only continent in which the Cerambycinae (550 spp.) exceed the Lamiinae (440 spp.). Prioninae are represented by 50 species in 21 genera, and flightless Lamiinae are numerous. The Aseminae and Callidiini, also predominantly northern groups, are also absent from Australia but represented in Madagascar and Chili by taxonomically isolated, presumably relict, genera. New Zealand has only about 250 known species (26, 155), the largest numbers of genera being apterous [e.g., *Somatidia*, *Hybolasius*, *Xyloteles*]. The Lepturinae, absent from Australia, are sparsely represented in New Zealand.

The Pacific islands in the area north and east of the Solomons to Easter Island and Hawaii are treated as Polynesian and oceanic by Gressitt (134). Perhaps the most interesting of the cerambycid faunas are found in the last-mentioned island group (304). Those of Micronesia are also disharmonic, lacking many of the dominant tribes in the Philippines and New Guinea and possessing largely oceanic genera with some flightless endemics (134). The Cerambycidae of the subantarctic islands, especially in the Atlantic are predominantly apterous.

The longicorns of Madagascar, like other elements in the insect fauna (251), are highly endemic and diversified (e.g., the distinctive Lepturinae with many monotypic genera).

LARVAL FOOD HABITS—GENERAL

Most larval Cerambycidae feed upon the solid tissues of living, dead, or dying plants or, less commonly, in rotten wood (23). For each species the limits are usually very exacting for normal development (78). Thus, the various stages of a gradually disintegrating tree have their particular species, some in the living parts, others in the recently dead material, and still others in the wood which has seasoned for several years (1, 292). As would be expected, their role in this succession varies from host to host and region to region (18, 24, 78, 83, 101, 130, 158, 166, 176, 246, 270, 281).

Many species attack living trees and shrubs, and scarcely any portion of the plant is immune. In North America, for example, smaller twigs and branches are girdled by the larvae of *Styloxus*, *Elaphidionoides*, *Aneflomorpha*, and *Xylotrechus quadrimaculatus* Haldeman (77, 78), and by the adults of *Oncideres* and *Oberea* (202, 275). Larger twigs and branches are de-

formed or killed by the larvae of *Saperda*, which cause abnormal tissue growth and gall formation (110). Some species (e.g., *Xylotrechus insignis* LeConte) bore into the living trunk through scars or the butts of broken branches. Others (e.g., *Pyrotrichus vitticollis* LeConte) destroy the heartwood of a tree but allow the living tissue to remain intact. The larvae of a number of the species which attack living trees, as *Goes*, *Hammoderus*, and *Saperda*, will die if the tree is cut before they mature. A few, such as *Encyclops* and *Microcyltus* (77) and *Physocnemum brevilineum* (Say) (139), feed in dry, scaly bark of living trees, causing abnormalities. Bark borers of the genus *Acanthocinus* incidentally are often very destructive to bark beetle broods (166). Species of *Prionus* may hollow out and kill the roots of living trees, *Desmocerus* those of *Sambucus* (50, 145). A comparatively few species live upon small annual or perennial plants. Thus, *Mecas* and *Crossidius* feed upon the roots of *Artemisia* and *Chrysothamnus* (211), *Tetraopes* those of *Asclepias*, *Anoplodera instabilis* (Haldeman) those of *Lupinus*, and *Brachysomida tumida* (LeConte) and *Cortodera berkeleyensis* G. Hopping those of *Ranunculus* (204). Finally, larvae of the prionine subgenus *Homasthesis* feed on the roots of sod-forming grasses.

In the tropics, a greater proportion of species are live-stem borers, perhaps, as pointed out by Vogt (*in litt.*), because of the intense competition for dead wood provided by termites (and in many areas by humans). He reports dead wood cerambycids more common in mangrove swamps, where the occurrence of termites is limited.

SYMBIOSIS AND DIGESTION OF WOOD

Intracellular symbiotes of Cerambycidae have been known since the time of Heitz (144) and Ekblom (102) who observed yeastlike organisms in the cells of the intestinal walls of *Rhagium*. Schomann (283), in the most thorough study that has yet been made of their occurrence in the family, found them regularly present in the Spondylinae and Aseminae, certain Cerambycinae (Saphanini, Trichomesiini, Tillomorphini, and *Dialges*, but not other Cerambycini), and most Lepturinae, except the Toxoti, *Vesperus* and *Pidonia*. Steinhaus (299, 300) has summarized available information on the mycetomes of Cerambycidae, which most frequently consist of small tissue masses or symbiote-filled evaginations of the gut wall which circle the gut in one or two girdles, become smaller during pupation, and are lacking in the adults. However, the symbiotes are retained in intersegmental pouches of the ovipositor, smeared on the eggs during oviposition, and enter the larva as it chews the chorion during eclosion.

The possible role of intracellular symbiotes in the digestion of wood by cerambycid larvae has been a matter of controversy (47, 48, 84, 85, 219, 250), and this aspect of the subject will not be reviewed here. However, it appears that those species the larvae of which live in fresh wood of deciduous trees lack intracellular microorganisms (at least yeasts), whereas those which attack coniferous hosts, living or dead, harbor symbiotes (283).

Most of our knowledge of digestive enzymes in Cerambycidae is less than 30 years old, although an enzyme hydrolyzing xylan was found in the alimentary tract of *Phymatodes* as early as 1905. Much of the present summary is condensed from Parkin (250).

In 1930, Falck (108) and Horn (151) analysed the food and frass of *Hylotrupes bajulus* (Linnaeus) and showed that during digestion depletion of cellulose and pentosans occurs. Subsequently, Schuch (284) demonstrated that some constituent of the cell contents is necessary for the best growth of the larva, since they grow much more rapidly when feeding in the outer zone of the sapwood than in the inner zone or in heartwood. Becker (16) observed accelerated growth when larvae were inserted into wood impregnated with peptone solution, but not in wood impregnated with soluble starch or glucose. Since an intermediate value was obtained with malt extract, he suggested that a small amount of nitrogenous matter may have been present. Grösswald (136) found that, 180 days after hatching, larvae in wood impregnated with 5 per cent diastase solution weighed up to 114 mg., while similar larvae in peptone-impregnated wood weighed up to 4 mg. and in the untreated controls up to 2 mg. Parkin (250) points out that this phenomenon could hardly depend upon the enzymic action of diastase on the wood starch, since the quantity present in softwood timbers is very small, but it is possible that the diastase contains as an impurity some growth-promoting substance, the presence of which enables the larva to utilize larger amounts of some or all of the major components of the wood.

Ripper (271) has demonstrated the presence of a cellulase in mid-gut fluid of larvae of *Cerambyx*, *Rhagium*, and *Leptura*, and Müller (238) showed by chemical analysis that there is a considerable loss in cellulose and pentosans from wood passing through the larval gut of *Oxymirus cursor* Linnaeus, *Leptura rubra* Linnaeus, and *Gracilia minuta* Fabricius. He also detected in the alimentary canal of *Oxymirus* the enzymes cellulase, hemicellulase, xylanase, amylase, invertase, maltase, emulsin, lipase, trypsin, and erepsin. Mansour and Mansour-Bek (219, 220) have shown that the larvae of *Macrotoma palmata* Fabricius and *Stromatium fulvum* Villers possess an enzyme hydrolyzing cellulose, but that *Xystrocera globosa* Olivier cannot secrete a cellulase and appears to derive its food from the minor carbohydrate constituents which occur plentifully in the sapwood in which it lives.

Parkin (250) tested the digestive juices of six species of cerambycid larvae (Table III) and found no fundamental difference between the digestive powers of species feeding upon bark, phloem, and cambium and those living in the solid wood (although larvae of *Smodicum* seemed to be deficient in enzymes hydrolyzing the cell-content carbohydrates). Judging from his rather uniform results and those of Müller (238), it appears likely that the majority of cerambycine and lepturine larvae digest the starch, soluble sugars, hemicelluloses, cellulose, and proteins in wood. However, relatively few genera are as yet definitely known to produce a cellulase. Mansour & Mansour-Bek (219) were unable to detect this enzyme in *Xystrocera glo-*

TABLE III

THE ACTION OF THE DIGESTIVE JUICES OF CERTAIN CERAMBYCID LARVAE ON VARIOUS SUBSTRATES*

	Starch	Sucrose	Maltose	Lactose	Cellulose	Hemi-cellulose A	Hemi-cellulose B	Protein
<i>Rhagium</i>	++++	++++	0	+++	+	++++	++++	++++
<i>Phymatodes</i>	++++	++++	+++	+++	++	+++	++++	+++
<i>Isotomus</i>	+++	++++	+++	+++	+	++++		+++
<i>Xylotrechus</i>	++++	++++	0	0	+	+++	+++	+
<i>Elytropses</i>	+++	+	++	++	+	++	++	+
<i>Smodicum</i>	0	0	0	++	+	++++		+

* After Parkin (250)

bosa and concluded that *X. globosa* is dependent for its food on cell contents. Savely (281) tested several phloem-feeding cerambycid larvae (*Monochamus*, *Acanthocinus*, *Callidium*, *Rhagium*, *Romaleum*) for a cellulase (and for intestinal protozoa which could be considered to play a part in nutrition). The results were negative for these but positive for *Derobrachus brunneus* (Fabricius). He commented on the fact that the larvae of this species are among the largest of the cerambycids and feed in both rotten pine and oak. In pines he found them feeding on wood in a very advanced stage of decay; in oak they were feeding on the solid heartwood of a rotten log that had been dead about five years and in sapwood attacked by "white-rot" fungi. No intestinal protozoa or bacteria were found in their gut that could account for the presence of cellulase. Haliburton (139), in Canada, noted that the larva of *Physocnemus brevilineum* (Say) found partially desiccated elm phloem tissue nutritionally superior to dead and dry tissue of similar origin in outer bark. He was unable to determine what the larva assimilated from the tissue, which was negative to tests for starch.

HOST SPECIFICITY

Host specificity in varying degrees is characteristic of Cerambycidae and has undoubtedly been an important factor in their evolution [Linsley (206, 207, 214)]. Generally speaking, the more primitive groups are the more polyphagous (e.g. Parandrinae, Prioninae, Lepturinae), although some more specialized forms of restricted host range occur among them. Further, the polyphagous species are usually associated with wood which has been dead for some time or is actually decomposing. These species may be able to develop on wood of either coniferous or nonconiferous origin, but most polyphagous species are limited to either the gymnosperm or angiosperm hosts. Sometimes this distinction is made at the level of higher taxa (e.g., the Spondyliinae, Aseminae, and the less specialized Callidiini are limited largely to conifers, most Lamiinae and the more specialized Cerambycinae are restricted to angiosperms). Within the Gymnospermae a sharp host-plant dis-

inction is usually made between the group represented by the Taxodiaceae-Cupressaceae and that of the Pinaceae. Sometimes this distinction is evident at the generic level (e.g., *Atimia*, *Callidiellum*), and in other cases at the species level (e.g., *Callidium*, *Semanotus*). In general, those species which develop as larvae in living trees (e.g., certain *Saperda*) are usually the most narrowly host specific. One of the most polyphagous species is the Indian cerambycine *Stromatium barbatum* (Fabricius), which has more than 300 recorded hosts, including both broadleaf trees and conifers, but it attacks dry wood, including seasoned timber (21).

The significance of host selection among Cerambycidae and other phytophagous insects was apparently first visualized by Walsh (317), who saw in host preferences, reinforced by inheritance, the beginnings of divergence ultimately leading to separate species. His conclusions were formalized by Hopkins (150), in connection with surveys of bark beetle damage, into a principle which states, in effect, that in an insect species capable of breeding in two or more hosts, individuals will normally continue to select the particular host species in which they passed their own life cycle. If this "host-selection principle" is valid, the evolutionary results would provide, at least in the early stages, physiological strains and races with particular host preferences (306) and, subsequently, sibling species and distinct morphological species (226). However, Peyerimhoff (256) does not accept the host-selection principle, and interprets the ideas of Hopkins and Craighead as favoring the inheritance of acquired characters. Citing examples of biological races or subspecies, he concludes that host selection involves a combination of factors, including the attractiveness and condition of the host, internal factors of the plant feeder (including mutation), as well as environmental conditions. However, host selection (see below) and host specificity, although interrelated, are not necessarily the same thing. The latter defines the range within which the former usually takes place.

Experimental evidence to test these viewpoints remains largely inconclusive, in part because of the difficulty of rearing cerambycids under controlled conditions that duplicate those obtaining in the natural habitat, and in part because of problems of taxonomic interpretation. However, Crawshaw (79) who found *Tetropium gabrieli* Weise exclusively on *Larix europaea* in the wild state, when he confined females with *Picea* and *Pinus*, was able to force successful attack and obtain subsequent larval development. Craighead (76) designed a more comprehensive series of experiments in order to test the application of the basic host-selection principle of Walsh and Hopkins in the family Cerambycidae and came to the following conclusions:

(1) In practically all the species experimented with, the adults show a marked predilection for the host in which they have fed as larvae, provided they are not deterred by other factors, such as the unfavorable condition or the small quantity of the host; (2) there is considerable variation in the degree of preference for the original host as between different species, thus—(a) certain species are capable of

living in only one genus or species of plant, which consequently they select; (b) certain species, chiefly those living in nature in several hosts, can be forced to adopt a new host; (c) certain species, chiefly those feeding in nature in a great variety of plants, show little discrimination in the selection of hosts; (d) certain species feeding in nature in a great variety of hosts often show a preference for a few of these; (3) in forced transference of individual adults of a species to a new host, a high mortality of the broods usually occurs, especially in the case of eggs laid by beetles emerging from the original host, in which case the mortality is often total; one-half to full-grown larvae, however, usually can be successfully transferred to a new host and live and transform to adults; (4) with some species that can be reared in a secondary (new) host, by the larvae feeding one or part of one year, preference for that host is shown by the resulting adults; (5) in general, the fewer the hosts in nature, the more marked the predilection for a particular host, and vice versa; (6) continued breeding in a given host intensifies the preference for that host; (7) the condition of the host has a great influence on host selection, in that every species prefers an optimum condition of the host which it selects and will choose a new host in the optimum condition in preference to an old host in which the conditions are unfavorable; (8) the quantity of wood at the disposal of the ovipositing adults may influence the insects in their choice between different kinds of host wood, in that, if there are many adults to a limited amount of the primary host, some species will select a secondary host if such is available; if this is done, however, the resulting brood is weakened.

Duffy (93), utilizing the results of rearing experiments and field observations on British species, came to somewhat different conclusions:

(1) Ovipositing adults are influenced to a greater degree by the nature and condition of the host (i.e. thickness of bark, stage of decay, moisture content) than by the identity of the host species . . . ; (2) ovipositing adults (at least under laboratory conditions) are influenced by the amount and variety of hosts, irrespective of species . . . ; (3) the successful development of larvae depends to a far greater extent upon the nature and condition of the wood than upon the host species concerned . . . ; (4) many species [show] a marked preference for a particular part of a tree . . . and (5) the range of hosts is, in general, greatest in species which oviposit on freshly cut, slightly injured or decaying wood; whereas the hosts of species which oviposit only on healthy living wood or plant tissue are considerably restricted, often to a single genus.

Much more data, derived from both field and laboratory experimentation, are needed on the subject, especially in relation to species associated with living and freshly cut trees. Special attention should be given to sibling species, host strains, and geographical races in such groups as *Callidium*, *Xylotrechus*, *Neoclytus*, and *Saperda*. There is reason to believe that certain "species" which appear to have a wide host range may actually consist of a series of sibling species or potential sibling species in the form of host strains. There is much evidence in the Cerambycidae of abrupt and sudden changes of host plants (e.g., the species of *Atimia* are limited to the Taxodiaceae and Cupressaceae, but the closely related *Paratimia conicola* Fisher lives in pine cones). Further, closely related sibling species are usually sympatric with quite different host plants, but closely related

allopatric species usually have identical or closely related host plants. This suggests that host specificity may sometimes result in sympatric speciation.

Generally speaking, the host-specific Cerambycidae are sympatric with their host plants, but the two ranges rarely coincide. Discussing the distribution of forest Cerambycidae in India, Stebbing (298) points out that the habitat of the same species of tree may vary from a comparatively hot, dry climate to a hot, moist one, as the sal (*Shorea robusta*) in the Central Provinces and in Assam. Some of the species which infest the tree in the hot, dry climate have also become adapted to the hot, moist one. Although *Hoplocerambyx spinicornis* (Newman) infests this tree both in the Central Provinces and in Assam, it extends southward far beyond the range of the sal to attack *Duabanga sonnatioides* and *Pentacme suavis*. On the other hand, the range of *Hoplocerambyx* does not extend with the sal tree into Northern India; in the foothill forests of the Western Himalaya, it is replaced by the related longicorn *Aeolesthes holosericea* (Fabricius).

The evolutionary significance of host specificity in common with partial geographic isolation is evident in the Hawaiian Islands. Nearly 75 species of *Plagithmysus* and a few other very closely related genera are now known in this island group, the whole complex presumably having been evolved from a single clytine ancestor, possibly from America (323). The species are highly host specific, attacking dead and dying branches or sickly and fallen trees, and each is confined to a single island (303, 304). Thus, for example, the common and widespread *Acacia koa* is attacked by at least six species of *Plagithmysus* (two each on Oahu and Kauai, one each on Maui and Hawaii) and 11 species of *Neoclytarlus* (three each on Kauai, Maui, and Hawaii, two on Oahu). A similar relationship exists between *Pipturus pelea*, and other endemic Hawaiian trees, and various species of *Plagithmysus*, *Callithmysus*, *Paraclytarus*, and *Neithmysus* (the last restricted to *Pelea*). By contrast, most of the Cerambycidae which have been introduced to the islands through commerce are associated with introduced lowland trees, and the two endemic stocks of more generalized, polyphagous Cerambycidae, *Parandra* and *Megopsis*, have but a single species each throughout the islands.

ECONOMIC IMPORTANCE

The Cerambycidae comprise one of the economically most important groups of insects of the world (4). Since their economic importance is a reflection of their ecology, a brief review of the ways in which they compete with man is here included [for more detailed accounts see Duffy (93) and Linsley (212)].

Forests.—Cerambycidae, in the larval stage, are primarily borers in dead wood, and their ecological role, at least in the temperate forest, involves the reduction of dead and dying trees, broken branches, and slash. Likewise, a great number of neotropical species have "pruning" habits, and contribute to the "littering" of the forest. In the economy of the forest, these are beneficial roles. But when storms or fires sweep through forested regions

and blow down or scorch commercial timber, Cerambycidae may destroy the wood before it can be utilized (78) or may develop in salvaged lumber (169) and subsequently emerge from structural timber (100). Among species which attack living trees, many cause serious injury or death or attack wood with a high economic value to man (78, 106, 166, 293). Thus, one small outbreak of one species, affecting only eight square miles of forest, killed 45,000 trees aggregating nearly 1 million cubic feet of timber (4, 212). Cerambycids have also been implicated in the transmission of diseases of forest trees. Reid (267) records the association of *Monochamus* feeding scars with die-back of balsam fir. Isolations from the twigs involved yielded three fungi, *Thyronectia balsamea* (Cooke & Peck), *Micropera abietum* (Peck), and *Cystospora* sp.

In tropical regions, forest species are less well known, except in India, Burma, and Ceylon, where they are regarded as the most destructive group of forest insects. Beeson & Bhatia (21) have summarized data on 350 species associated with 568 species of trees, shrubs, and woody climbers. The sal tree has 37 species which attack it, and one dry wood borer, *Stromatium barbatum* (Fabricius), has 311 known food plants. More than 100 species injurious to forest trees in South America are enumerated by Costa Lima (70) and Bosc (32); numerous African species are recorded by Duffy (94).

Forest products.—Cerambycid larvae may cause serious defects in lumber, either by attacking living trees or by attacking shortly before cut logs are sawed. In temperate forests, the resultant reduction in grade probably causes a greater monetary loss than do the tree-killing species (78). Further, defects in living trees are frequently enlarged by other insects until the heartwood is completely destroyed.

Damage to seasoned lumber by round-headed borers may occur where lumber is seasoned or stored in open yards near forests (231). But since very few species oviposit on dry, barkless wood, few become domestic pests. An exception is the "old house borer" or "Hausbock," *Hylotrupes bajulus* (Linnaeus), which feeds in the sapwood and to a lesser extent in the heartwood of dry, seasoned, coniferous timber such as telephone poles, fences, and roof and attic supports (93, 97). The Indian *Stromatium barbatum* (Fabricius) also attacks wooden structures, including furniture, supporting timbers, panels, shelves, etc. (21, 105), as does the East Asiatic *Stromatium longicorne* Newman, especially in Taiwan and the Ryukyu Islands [Gressitt (*in litt.*)]. A number of other cerambycids infest wood prior to utilization and cause damage through subsequent emergence (77, 93, 96, 100, 153, 189, 205). Structural timbers in contact with the ground are also subject to direct attack, especially when old and moist (216, 218, 247).

Shade trees.—In temperate regions, round-headed borers usually attack shade trees only when other factors, such as defoliation, diseases, drought, frosts, or transplanting make them susceptible to attack (109, 146), and it is often difficult to place responsibility for the death of the tree (78).

However, Pechuman (252) considers feeding by adults of *Saperda tridentata* Olivier of primary importance in the transmission of Dutch Elm disease, and *Anoploclera nitens* (Förster) has been charged with carrying the spores of chestnut blight (131). In tropical regions, living shade and ornamental trees are attacked by a large number of Cerambycidae (21, 70, 94).

Fruit and nut trees.—Trees grown for fruit and nut crops, both native and introduced, are also widely attacked by cerambycids. Of 118 kinds of injurious Cerambycidae in Japan, 49 are associated with fruit and nut trees, including mulberry, and four with grape vines (293). In Australia (185), parts of Asia (86, 159), and in North America (77), the more important pome fruits are attacked by species formerly associated with native trees, as the *Amelanchier*- and *Crataegus*-infesting apple-tree borers (*Saperda* spp.) of New England (40, 147). In most areas where grapes are grown, various endemic Cerambycidae attack the vine (77, 225, 293). Several species of *Oberea* girdle stems of fruit and nut crops, one of the best known being the raspberry cane borer, *Oberea bimaculata* (Olivier), which is also injurious to perennial asters (156). Although fruit-tree injury is caused by larvae, adult Cerambycidae may scar the fruit surface (170) or burrow into soft fruits, such as ripening peaches (137).

By far the most important cerambycid pests are those which attack living tropical and subtropical fruit and nut trees (132, 163, 230, 241, 265, 266, 289), including cloves (162), coffee (68, 70, 196, 223, 315), cacao (68, 70, 272), fig (138, 152, 157, 164, 293) and citrus (57, 261, 288, 305, 318). Forty-eight species attack native and introduced species of *Coffea* in tropical Africa, and native species have taken to *Citrus* in most of the areas where it has been introduced. In eastern Asia, at least four of these are major pests (65, 132, 148, 198, 199), one of which, *Anoplophora macularia* Thomson, kills thousands of young trees [Gressitt (*in litt.*)] and in some areas infests 90 per cent of the remainder. Many other species are polyphagous and have turned to citrus from distantly related hosts (10, 70, 72, 95, 154), but in Australia *Citriphaga mixta* Lea overlaps from the desert kumquat (119) and *Uracanthus cryptophagus* Olivier from the native finger lime (244). Of the several species of longicorns attacking citrus in tropical Asia (66), some of the Callichromini are probably native to that host (177, 239, 263).

Although several polyphagous Cerambycidae attack palms in various parts of the world, relatively few species are regularly associated with this group of plants (190). At least three attack coconut in the South Pacific, and in Micronesia larvae of *Caroliniella aenescens* Blair bore in the petioles and midribs of the fronds while the adults feed in the unfolding buds (134). A few longicorns are associated also with the date palm in Asia Minor or North Africa.

Vegetable and field crops.—As pests of vegetable and field crops, cerambycids are less well known. Species of *Phytoecia*, which live in the stems of umbellifers and composites are capable of severe injury to seed carrots

(93, 167) and to Jerusalem artichoke (293), and have been accused of damaging cabbages (131). Other Lamiinae infest stems of sweet potato in Java (164), those of eggplant in British Guiana (67), and those of cucurbits in Argentina (32). *Ropica dorsalis* Schwarz and three species of *Apomecyna* bore in watermelon, muskmelon, and cucumber vines in China or Japan (132, 293, 294), and related species attack stems of French beans in Portuguese East Africa (280), of pumpkins and melons in the Sudan (259), South Africa (121), and Queensland (224). In southwestern United States, the larvae of *Dorcasta cinerea* (Horn) bore in stems of sunflower and other oil-seed crops, as do those of *Agapanthia dahli* Richter in the Ukraine (248). Similarly, *Ataxia hubbardi* Fisher infests stalks of cotton in Texas (234), as does *Tragiscoschema bertolonii* Thomson in Mozambique (197), and *Tragiscoschema wahlbergi* Fahr and *Volumnia westermanni* Thomson in Portuguese East Africa (280). In southern Europe, stems of wheat, barley, and rye are fed upon by larvae of *Calamobius flum* Rossi (131), and in North America the related *Hippopsis lemniscata* (Fabricius) attacks the stems of *Vernonia* and other plants (286). Stems of jack beans in Hawaii are infested with *Sybra alternans* Wiedemann (301).

A number of subterranean forms are injurious to turf and grass plots in North America (77) and Europe (131). The roots of maize are damaged by *Dorcadion* in Italy (131), those of sugar cane in China by larvae of *Philus* (132) and elsewhere by various Prioninae and Lamiinae (34). In the Mediterranean region, larvae of *Vesperus* are especially injurious to roots of alfalfa, root vegetables, and potato tubers (131). Other larvae feed in the roots of *Ferula* in Afganistan [Vogt (*in litt.*)] and sever the roots of hemp in Japan (175). Dry derris roots are also attacked by numerous Cerambycidae both in Asia (232) and in South America (90).

Seed-infesting species.—Although seeds of various plants, in particular conifers and legumes, are attacked by a great variety of insects, few are regularly utilized by Cerambycidae. A North American and an Indian species infest full-grown green or maturing pine cones (54, 111). *Lophopoeum timbouvae* Lameere feeds in the seed pods of various legumes in South America (32, 43, 71), as does a species of *Leptostylus* in Puerto Rico (322). A related species lives in the fruits of *Sapindus* in Brazil [F. Lane (*in litt.*)], and *Baryssinus leguminicola* Linell in the seeds of *Enterolobium* in Paraguay (64). In North America, *Lepturges spermophagus* Fisher infests unripened seeds in green pods of cowpeas in Mexico (112), and *Ataxia sulcata* Fallén and *Leptostylus terraecolor* Horn attack mangrove in Florida (77). In Africa, several small lamiines develop in dry coffee berries (3, 191), along with *Enaretta castelnaui* Thomson (94).

Orchids and flowers.—In Java, a larval *Diaxenes* lives in the fleshy roots of various orchids and the adults feed on young leaves, flowers, and fruits (117). Related species infest orchids in Burma and the Philippines (122, 302). Garden plants, especially those with woody stems, as roses and crotons, are also subject to attack (142, 287), as are asphodels, hellebores, and

euphorbias (131, 316), and also ornamental umbellifers, borages, and composites (131, 132, 293).

Opuntia cactus.—Cerambycidae have been intentionally introduced into Australia and South Africa to combat escaped cactus in range lands (88, 254, 255). Two species of *Moneilema* and a *Lagocheirus* were introduced into Australia from Texas and Mexico and apparently established, but proved of minor importance (88). *Moneilema ulkei* Horn was reared in South Africa but apparently never released (191). *Lagocheirus* were released, but the populations have continued to decline. Weber (319), Dodd (89), and Fullaway (120) record the release of *Moneilema* and *Lagocheirus* from Australia on the island of Hawaii to suppress the tree cactus, with indications that *Lagocheirus* at least, would become established, as it has in Australia (192). More recently, *Aerenicopsis championi* Bates and *Plagiohammus spinipennis* (Thomson) have been introduced from Mexico as potential agents for the biological control of lantana [Weber (319); Gressitt (*in litt.*)].

ETHOLOGICAL AND PHYSIOLOGICAL ADAPTATIONS OF ADULTS

Emergence and seasonal distribution.—In normal years, emergence is characterized by a definite succession of forms. For instance, in California, at lower elevations and in the more southerly parts of the state, the first species appear in February and March (occasionally earlier) and include *Neoclytus conjunctus* LeConte, *Cortodera* spp., *Atimia* spp., and *Lophogonius crinitus* (LeConte). These are followed in late spring and early summer by species of *Brachysomida*, *Anoplodera*, *Leptura*, *Xylotrechus*, *Synaphaeta*, and others. In midsummer only a few new forms—including *Methia*, *Styloxus*, and *Aneflomorpha*—first appear, but in the fall there is a renewal of activity with the emergence of *Crossidius* and the second broods of *Atimia dorsalis* LeConte and *Saperda hornii* Joutel, etc. At higher elevations and in the northern and cooler parts of the state, the season is much shorter. The earliest forms, such as *Rhagium* and *Spondylis*, usually do not appear until May or June, and the late forms begin to disappear in August. In eastern North America the majority of species are active in June and July (249). However, the fall-emerging *Megacyllene robiniae* (Forster) may be found as late as November (173). In India, four emergence periods, based on climatic factors, have been defined by Beeson & Bhatia (21). The temperate summer-emergence period involves various endemic genera found in the mountains which attack living trees, as well as dead wood borers in genera with northern, Holarctic affinities [e.g., *Arhopalus*, *Purpuricen*, *Tetropium*, *Molorchus*, *Prionus*]. The pre-monsoon or dry-season emergence period of the submontaine and plains regions brings forth such species as *Glenea spilota* Thomson (Fig. 1); the monsoon period, initiated by the southwest monsoon, and the post-monsoon season or autumn of South India each are characterized by the emergence of certain species. Those that emerge at the beginning of the monsoon period are influenced by the date of arrival of the monsoon and the quantity and distribution of the rainfall.

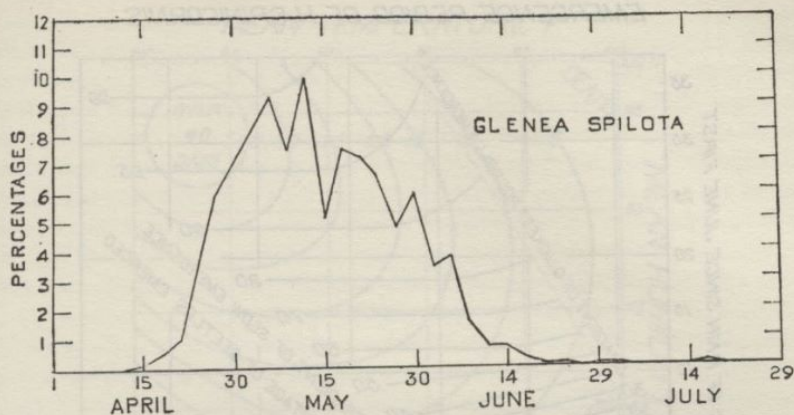


FIG. 1. Emergence of *Glenea spilota* Thomson, a dry season species, plotted at three-day intervals. [After Beeson & Bhatia (21)] Compare with *Hoplocerambyx spinicornis* (Newman) (Fig. 2, 3), a typical wet-season species.

Thus, 10 inches of rain will bring forth from 97 to 100 per cent of the adults of *Stromatium barbatum* (Fabricius) and from 30 to 59 per cent of *Hoplocerambyx spinicornis* (Newman). When 30 inches of rain have fallen, 93 per cent of the *Hoplocerambyx* will have emerged (Fig. 2). However, since monsoon precipitation is uneven, emergence is uneven, and the beetles respond to each shower or storm (Fig. 3).

Longevity.—Little is known of the natural longevity of emerged adult longicorns. The limited feeding of many species suggests that they are probably short-lived. Craighead (73) reports that certain Prioninae have been kept alive without food for 30 to 40 days, but so long a life span is probably exceptional for the family. Beeson & Bhatia (21) were able to keep adults of *Hoplocerambyx spinicornis* (Newman) alive for 10 to 14 days without solid food or water. Still, water is necessary, and without it adult life is reduced by 10 days or more. The normal adult food is bark, particularly living inner layers, and sap, which is imbibed until the alimentary canal is fully distended. After gorging on sap the beetles appear intoxicated and often are unable to stand or fly. The longest life of adults in captivity was 49 days for the male, 38 days for the female (Fig. 4). Under laboratory conditions, with food provided, the writer has found various Aseminae and Cerambycinae relatively short-lived, often surviving only two or three weeks, in which time mating and oviposition took place. Some of the Lamiinae, however, survived for several weeks under laboratory conditions, and there are indications that adults of this subfamily are generally longer lived. With food provided, adults of *Diaxenes* have survived for three months in the laboratory (117), and under optimal conditions those of *Dihammus cervinus* Hope may live for 17 weeks and *Batocera rufomaculata* DeGeer for eight months (21). In the Cerambycinae, males are often

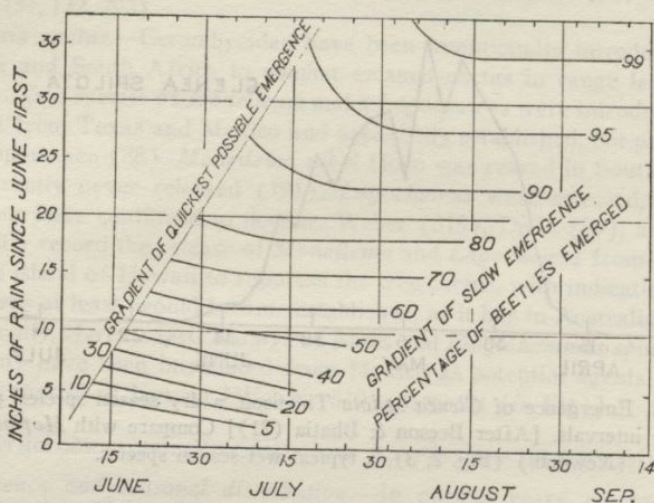
EMERGENCE PERIOD OF *H. SPINICORNIS*

FIG. 2. Correlation between number of inches of rain falling since June 1, the date, and the percentage of the total annual population of *Hoplocerambyx spinicornis* (Newman) emerged. [After Beeson & Bhatia (21)]

shorter lived than the females, and after they have accomplished their sole function, that of fertilization, death may ensue rather quickly. However, those of *Hylotrupes bajulus* (Linnaeus) live on the average about twice as long as females (e.g., 16:8 days). At low temperatures (11°C.) the life of both sexes is prolonged and the difference less marked (97).

Longevity in adult Cerambycidae can also be profoundly influenced by

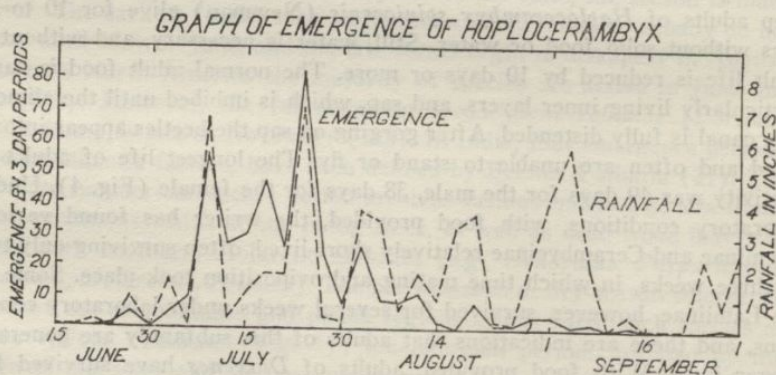


FIG. 3. Correlation between emergence of adults of *Hoplocerambyx spinicornis* (Newman) at three-day intervals and rainfall for the same intervals. [After Beeson & Bhatia (21)]

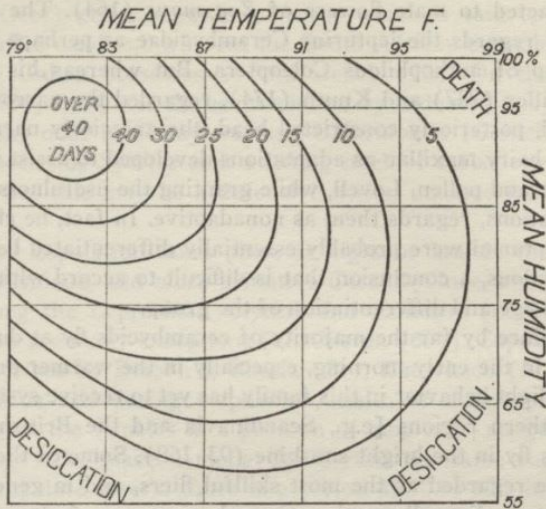


FIG. 4. Zones of maximum life of adult beetles of *Hoplocerambyx spinicornis* (Newman) at different combinations of temperature and relative humidity. [After Beeson & Bhatia (21)]

physical factors in the environment. Thus, *Hoplocerambyx spinicornis* (Newman) finds low humidities unfavorable at both low and high temperatures, and in dry air the beetle dies of desiccation (Fig. 4). High temperatures speed metabolism and reduce life proportionately. For this species, the most favorable temperatures are in the vicinity of 80°F. at relative humidities of 88 to 98 per cent.

Feeding.—Although some Cerambycidae (e.g., *Hylotrupes*, *Stromatium*) appear to require little or no food in the adult stage, for most species some feeding appears to be an essential prerequisite to egg maturation and oviposition. According to Schwarz (285), *Dendrobias* are especially fond of printer's ink and sometimes obliterate the large letters on advertising posters. *Monochamus* have been accused of injury to rayon dresses (128). Most species, however, utilize more conventional foods, and have been classified by Butovitsch (51) as follows: (a) flower feeders on pollen, stamens, nectar, etc. [most Lepturinae, certain Cerambycinae, a few Lamiinae]; (b) bark feeders on thin bark, bast, twigs, branches, trunks [Lamiinae]; (c) leaf feeders on foliage, leaf stalks, etc. [Lamiinae]; (d) pine needle and cone feeders [e.g., *Monochamus*, *Acanthocinus*]; (e) sap feeders [some Lepturinae (e.g., *Rhagium*), many Cerambycinae]; (f) fruit feeders [a few Cerambycinae, many Lamiinae]; (g) root feeders [*Dorcadion*, *Vesperus*, etc.]; and (h) fungus feeders [certain Lepturinae and Lamiinae].

Flower feeders are especially attracted to Umbelliferae, Compositae, and Rhamnaceae (143), although the Javanese lamiine *Prosoplus banki* (Fabri-

cius) is attracted to male flowers of *Zea mays* (164). The floreoecologist Lovell (215) regards the lepturine Cerambycidae as perhaps the most significant group of anthophilous Coleoptera. But whereas his predecessors, including Müller (237) and Knuth (174), regarded the narrow body form, the elongated, posteriorly constricted head, the anteriorly narrowed pronotum, and the hairy maxillae as adaptations developed to assist in the extraction of nectar and pollen, Lovell, while granting the usefulness of the structural modifications, regards them as nonadaptive. In fact, he claims that the genera of Lepturini were probably essentially differentiated before they became anthophilous, a conclusion that is difficult to accord with known facts regarding the age and differentiation of the group.

Flight.—Since by far the majority of cerambycids fly at dusk, or during the night, or in the early morning, especially in the warmer and more tropical regions, flight behavior in this family has yet to receive systematic study. In more northern regions [e.g., Scandinavia and the British Isles], most of the species fly in the bright sunshine (93, 168). Some of the flower-visiting forms are regarded as the most skillful fliers, and in general the more brightly colored, diurnally active Cerambycinae are faster of movement than the nocturnal forms. Nonetheless, the flight of by far the majority of the members of the family is relatively slow, quiet, and more or less direct, although many of the larger types, especially in the Prioninae, are lumbering, awkward and noisy fliers.

Assembling and mating.—Males of a given species usually emerge before the females and are the active agents in sex location. In many Cerambycinae, copulation may take place shortly after emergence from the pupal cell (28, 321) but in the Lamiinae usually awaits an interval of adult feeding (21, 264). Since the site of mating, except in flower-visiting types, is usually on the host plant, sex location and host selection are sometimes intimately associated, and the sex location may precede and determine the choice of host. Sex location is aided by olfactory organs in the antennae, and males may be attracted over long distances to tethered females (258). But while the olfactory sense appears to guide the males to the immediate vicinity of the females, other senses may play a role in the final contact. Heintze (143) found that males of flower-visiting Lepturini recognized females only by touching them with the antennae and lost interest in them after both antennae (but not one or simply the outer portions) were removed.

Apparently all members of the cerambycine tribe Callichromini produce a penetrating sex attractant variously described as resembling musk or attar of roses. The aromatic glands are located on the metasternum near the hind coxae (282, 295) and are present in several of the tribes of the cerambycine series (186). The scent emitted by the willow-feeding *Aromia moschata* (Linnaeus) is said to contain salicylic ester (149) and is not only detectable by humans at a distance of several yards (92) but is apparently capable of "stupifying" certain Diptera (104). *Mallambyx raddei* Blessig also appears to be odoriferous [Gressitt (*in litt.*)]. The lamiine *Agapanthia villosoviri-*

descens (DeGeer) emits a powerful scent which is said to resemble the smell of "snuffed candles," whereas the South African cerambycine *Xystrocera nyassae* Gahan possesses a fetid stench (93). On the other hand, Kalshoven (164) compares the scent emitted by Indonesian *Xystrocera* spp. with the musky odor of *Pachyteria* and *Chloridolum* (Callichromini). The Australian species of *Syllitus* emit a strong smell of carbolic when disturbed or captured, but this may be a defensive action unassociated with sex attraction (227).

The act of copulation takes place at night or late in the day in most Prioninae, Aseminae, and more primitive Cerambycinae, and during bright sunlight among the Lepturinae, Clytini, and Callidiini [cf. Rungs (277)], although there are many exceptions [cf. Cheron (60)]. Copulation behavior has been described by Beeson & Bhatia (21), Butovitsch (51), and others. After copulation and during oviposition, males of many species maintain attendance upon the females in a position of amplexus, suggesting that repeated matings take place. Among the Clytini the same pairs have been observed to copulate several times in a period of 10 to 15 minutes (51, 98). Since cerambycids cannot be disturbed readily during copulation and subsequent attendance, these facts assume considerable ecological importance.

Competition for females is often violent among the Prioninae and Cerambycinae, and mutilation is particularly common among males of these and other longicorns with prognathous or partially prognathous mandibles (21, 98, 233). The Lamiinae, which have vertical or retracted mandibles, usually butt or push one another until one of the opponents departs (240, 320). In *Hylotrupes*, the sexes attack each other before mating, and records exist of "courtships" in which all the legs of a female were amputated (97). In captivity, large males of *Hoplocerambyx* have been observed to monopolize several females, driving off smaller males (21).

In *Monochamus*, males of one species have been reported in attendance upon females of another (235), and two species may sometimes behave as one population, occurring on the same host at the same time and place (125). Interspecies matings and attempted matings have also been reported in the Lepturini (258), as has an interfamilial mating between a male cantharid (*Rhagionycha fulva* Scopoli) and a female cerambycid (*Clytanthus herbsti* Brahm) [Niesiolowski (243)].

Males of certain Cerambycidae, especially Clytini are attracted in late afternoon and evening to the leaves of certain broadleaved plants, such as *Verbascum*, which do not serve as host plants and are rarely visited by the female (297). Beeson & Bhatia (21) found 96 species in 58 genera consistently frequenting the foliage of sandal (*Santalum album*). These were diurnal, sun-loving species which do not feed on sandal as larvae or adults.

Attraction to host plant.—The facility with which host selection is accomplished in this family is undoubtedly a result of high development of special sense organs. Most of these organs are found in the antennae. Although the loss of a single antenna appears to have little effect on either

sex location or host selection, the loss of both structures greatly impairs or inhibits both of these functions. Without any doubt, the olfactory sense is one of the most important concerned. There is a definite succession of species which visit timber after cutting, and the species which arrive a day or so after felling are quite different from those which appear a week or two later. Apparently the chemical changes which take place in the wood have a selective influence upon the beetles. Bait pans designed for the attraction of Cerambycidae likewise exhibit selectivity in different stages of fermentation.

The olfactory sense is well developed in the Cerambycidae and several authors have commented on the speed of their reaction to certain odors. In particular, Stebbing (298), Beeson (19), and Beeson & Bhatia (21) have emphasized the immediate response of *Hoplocerambyx spinicornis* (Newman) to the fresh sap of *Shorea robusta*, to which adults fly from considerable distances; they have been attracted over a measured distance of a quarter of a mile within five minutes, flying upwind. Single trap trees have attracted 836 adults over a period of several days, 465 in a single day. The beetles approach upwind, the males preceding the females. Since such trees attract for only a quarter of a mile or so to the leeward and are almost nonfunctional to the windward, the numbers indicate considerable flight activity by the beetles while seeking an appropriate host.

Fermenting baits have long been used as a means of attracting adult Cerambycidae (55, 56), as have natural sites of oozing sap (311) or blazes especially prepared (307). Chemsak (59) records the attraction of large numbers of both sexes of *Dendrobias mandibularis* Serville and two females of *Eustomula validum* (LeConte) to watermelon rinds at a roadside picnic stand in Arizona.

Fermenting baits are most attractive to species which normally infest broadleaved trees and shrubs, less so to species which breed in conifers. However, Becker (16, 17) found pine oils containing the terpenes α -pinene and β -pinene attractive to ovipositing females of *Hylotrupes*, and Gardiner (126) succeeded in attracting large numbers of conifer-infesting species in Quebec with turpentine.

Infestations of *Saperda calcarata* Say in poplar are often characterized by "brood trees" (253). Such trees are usually larger than average for the stand and have shown good growth. Once such trees become infested, the borer population builds up rapidly and heavy re-infestation occurs until the host is no longer suitable for larval development. Dead trees are never attacked by this species, and only late-stage larvae can survive in cut wood.

Sound production.—Most adult Cerambycidae possess the power of stridulation (222). In the Aseminae, Cerambycinae, Lepturinae, and Lamiinae, this sound is produced by friction between the inner edge of the posterior margin of the prothorax and a specialized striated area on a median anterior prolongation of the mesonotum (91). This stridulatory plate varies from group to group and has been extensively used in the classification of genera and tribes (186), less commonly at the species level (207). In the huge

North African lamiine *Petrognatha gigas* (Fabricius), which produces a "vigorous, but otherwise harmonious stridulation," the area bears some sixty transverse striae that are very close together; in *Phrynetta aurocincta* Guérin, which produces an extremely shrill sound, the plate is very elongate and from 180 to 200, very fine, close, distinctly elevated striae are involved (191). In the subfamily Prioninae, no mesonotal stridulatory plate is present, and sound is produced by rubbing the posterior femora against the edge of the elytra (221). The Hawaiian clytine genus *Plagithmysus* utilizes both methods of sound production (290), and a special "drum" has been described in *Nothorhina* by Faber (107).

Since both sexes usually stridulate when captured, the function is commonly regarded as defensive [Duffy (93)], but it is possibly involved in sex location also [Alexander (2)]. Beeson & Bhatia (21) state that males of *Hoplocerambyx spinicornis* (Newman), when courting, sometimes raise the body to the full extent of the legs and stridulate. In the Madagascan genera *Ranova*, *Leucographis*, and *Lasiocercis*, the striae are coarser in the male (123). Sexual dimorphism in the stridulatory apparatus is also evident in some of the Lepturini [Kaszab (165)].

Cheesman (58) records that vast numbers of longicorns were attracted to a girdled tree in the Society Islands and in flight produced a humming so loud that they were mistaken for a swarm of bees. Similar observations have been made elsewhere, suggesting that the sound may assist in host attraction.

Oviposition.—Butovitsch (51) has made a careful analysis of the oviposition habits of the Cerambycidae and has proposed two major types. The first is: *oviposition exclusively with the aid of the ovipositor* (most Parandrinae, Prioninae, Spondylinae, Aseminae, Lepturinae, Cerambycinae), either (a) on the bark or outer surface of the host [e.g., *Spondylis* and a few Cerambycinae] or (b) in bark cracks or under bark scales [usual method for most forms which utilize the ovipositor only] or (c) in cracks and crevices in wood [a few Aseminae and Cerambycinae, e.g., *Arhopalus*, *Hylotrupes*, *Stromatium*] or (d) in entrance, emergence or ventilation holes of other insects [e.g., certain Prioninae, Lepturinae, Cerambycini, etc.] or (e) in the soil [primarily Prioninae] or (f) on the surface of various objects other than the host [*Vesperus*]. The second type is: *oviposition with the aid of the ovipositor and mandibles* [Lamiinae], either (a) in egg niches without special preparation of the substrate [most Lamiinae]—in which case they may be (1) in egg niches prepared by the mandibles [e.g., *Plectrodera*, *Phrynetta*, *Oncideres*, *Saperda*, etc.] or (2) in egg niches prepared by the ovipositor and mandibles [*Acanthocinus*]—or (b) in egg niches cut by the mandibles or drilled with the ovipositor with special preparation of the substrate [certain *Phytoecia*, *Oberea*, gall-forming species of *Saperda*].

Thus, the least specialized groups morphologically have the simplest oviposition habits; in some of the Prioninae and Lepturinae little more than imbedding the eggs in soft, decomposing wood is involved. The most spe-

cialized habits are found in the Lamiinae, which frequently utilize the mandibles to prepare the oviposition site. Trägårdh (313) associates this habit with the form of the lamiine head, which, with the retracted face and unusually powerful, somewhat oblique mandibles, is one of the basic features of the subfamily.

Although each of these methods of oviposition has special ecological significance, perhaps the most interesting is the girdling habit of the *Oncideres* and their relatives. The parent beetles completely girdle twigs and branches (some species use only those an inch or two in diameter) oviposit in the section beyond the girdle, thus providing freshly killed tissue in which the larvae can develop. Certain species, as *Oncideres dejeanii* Thomson, transversely groove or scar the bark adjacent to the egg site to loosen it for the young larva (180). In temperate regions the twigs and branches usually remain attached to the trees during the summer months and obtain moisture from the tree; they fall to the ground in the autumn winds, when they may be protected during the winter by a covering of leaves. Linsley (208) has pointed out that this habit has considerable ecological significance for other wood-boring insects which avail themselves of the niche provided by *Oncideres*. Fonseca (115), Bruch (44), Bosc (32), Lane (180), and Bondar (30) have briefly discussed the habits of *Oncideres* ("serradores") which girdle Argentine and Brazilian fruit and forest trees. Although some species have wide host ranges, many are associated with native Leguminosae. The North American species also (208) are largely attached to legumes, but one species attacks oaks, and the notorious "twig girdler," *Oncideres cingulatus* (Say), is a serious pest of pecan, hickory, and persimmon, and certain other fruit and ornamental trees. *Oberea*, *Nupserha*, and relatives are also twig girdlers and include numerous species of economic importance in Europe (9, 245) and Asia (99).

Overwintering and hibernation.—Overwintering among the Cerambycidae of temperate regions is normally accomplished by the immature stages or by unemerged adults within the pupal cell. Although Duffy (93) claims that "strictly speaking, cerambycids do not hibernate," *Apomecyna binubila* Pascoe in South Africa (121), *Aulaconotus pachypezoides* Thomson in Japan (175), and possibly the European *Pogonocherus hispidus* Muller (46), as well as several North American species [mostly wingless Lamiinae of the genera *Ipochus*, *Plectrura*, *Moneilema* and *Psenocerus* (140, 187, 204)], are known to live as adults from one season to another. Adults of other Nearctic species are occasionally encountered in the winter months, particularly in the warmer areas, but these usually may be accounted for by abnormally early emergence (204). Even in British Columbia, *Atimia dorsalis* LeConte has been taken in flight as early as March 20 (188). Winter activity of adult cerambycids is common in southern Florida (27) and other areas where freezing temperatures seldom occur.

STRUCTURAL ADAPTATIONS OF ADULTS

Body size and form.—Cerambycids include some of the smallest and the largest beetles known. In North America, *Cyrtinus pygmaeus* Haldeman may be less than 2 mm. long, and *Prionus californicus* Motschulsky and *Ergates spiculatus* LeConte occasionally exceed 60 mm. The largest European species, *Cerambyx cerdo* Linnaeus, attains more than 50 mm. But it is in the tropics that species attain the greatest size. The South American *Psalidognathus superbus* Fries, including the exerted mandibles of the male, reaches 65 mm. *Acrocinus longimanus* (Linnaeus) has forelegs which, in the male, may surpass 75 mm., with both femora and tibia as long as the body. *Batocera wallacei* Thomson, of New Guinea, may have a body length of 80 mm. with forelegs 85 mm. and antennae in excess of 190 mm.; the Neotropical *Macrodontia cervicornis* (Linnaeus) reaches nearly 170 mm., with mandibles (nearly 60 mm.) longer than the head and thorax combined (310). The Fijian *Xixuthrus heros* (Heer), the Malasian *Xixuthrus microcerus* (White), and the Brazilian *Titanus giganteus* (Linnaeus) reach 135 mm., 120 mm., and 160 mm., respectively.

In form, the majority of species are elongate and often subcylindrical; but those living under bark may be flattened, as *Smodicum*, twig inhabitants may be extremely slender, as *Spalacopsis*, and others may be variously modified in a cryptic manner (see below, p. 122). Cerambycids also exhibit a marked tendency to develop spines, especially on the pronotum, elytra, and appendages, but less commonly on other parts of the body; presumably these have adaptive significance. In some cases they contribute to cryptic form and coloration, but they may have a more significant function in protecting from predators [F. Lane (*in litt.*)].

Sexual dimorphism.—Sexual dimorphism is most commonly reflected in greater length of the male antennae which provides increased sensory area to assist in location of the female, in the relatively larger head, the somewhat narrower elytra, and the smaller, straighter, and less convex abdomen (49). In general, this dimorphism reaches its greatest development and diversity in the Prioninae males (6, 52, 179). The mandibles may be greatly enlarged (e.g., in the African *Jamwonus*) or excessively long and falciform so that they exceed the rest of the head (e.g., in the Neotropical *Macrodontia*). The longer antennae may be serrate, pectinate, imbricate (e.g., in many *Prionus*), or flabellate (e.g., in the Australian *Rhipidocerus* and *Enneaphyllus*, the African *Tereticus*), with the rami very long (e.g., *Closterus*) or biflabellate (e.g., the Neotropical *Sarifer flaviramus* Kirsch). Areas of specialized punctation may be present on various parts of the body (in the male of *Xaurus bennigseni* Lameere such areas are found on the antennae, legs, prothorax, and sternum). Areas of special pubescence or pilosity may exist on the body and appendages (e.g., the abdomen in *Macrotona*, the prothorax in *Tragosoma*, the tibiae in *Psalidognathus*). The vari-

ous pairs of legs may be of disproportionate length (e.g., *Macrotoma hayesi* Hope) or individual parts of the leg may develop more than the others (as the spined trochanters of some Anoplodermini, the reflexed femora of *Acanthophorus*, the curved tibiae of *Prionoma*, and enlarged tarsi of *Titanus*).

In some of the Anacolini and in *Prionapterus*, the males are smaller than the females and the elytra are abbreviated and dehiscent so that the wings are exposed; the two sexes are so different in form that they have even been described as separate genera (e.g., *Poekilosoma* Serville and *Cerocatenus* Serville). One of the most striking of these, the Columbian *Udeterus brequeti* Thomson, has elytra less than half as long as the body.

Males of *Tillyardia gigas* Carter have the palpi enlarged into open-ribbed, basketlike organs (53) and fly swiftly like cockchafers over dew-covered grasslands on the Dorrigo Plateau of New South Wales (307). In the New Guinean lamiine, *Giganteopalpus helleri* Franz, the male palpi are enormously elongated and slender (118); in the Neotropical *Heteropalpus pretiosus* Buquet, they are branched and hairy. The Micronesian *Acanthosciades* exhibit erect compressed spines on the elytral disc in the male (134). In other Lamiinae, sexual dimorphism is expressed in such features as fringed fore-tarsi in the male and sexual pilosity on the sterna in the Acanthoderini, etc. In the Cerambycinae sexual pubescence is also present on the abdomen of male *Eburodacrys* (229), and the abdomen is fringed in female Obriini and Stenaspini.

Cryptic coloration.—The majority of the adult Cerambycidae are nocturnal or crepuscular in habit, and this fact is usually reflected in their coloration. Those forms which secrete themselves during the day beneath logs, under loose bark, at the base of trees, etc., are commonly dull brownish or black (e.g., most Prioninae, Aseminae, Cerambycini, Phoracanthini). Those which remain inactive and exposed, or become active late in the day are usually cryptically colored, often blending so well with their surroundings as almost to defy detection. Most Lamiinae and some Cerambycinae exhibit this protective or habitat coloration, usually expressed in a mottled appearance resembling the bark of trees. Not uncommonly, especially in tropical forms, elaborate modifications of form, coloration, and pubescence contribute to a marked resemblance to lichens or moss, as the mosslike African *Petrognatha* (193), the American *Desmiphora*, *Ischnolea*, and *Orteguaze* (184, 229) and the New Zealand *Agapanthida*. This last, together with a moth in the same habitat, is a glaucous green, like the lichens in which it lies concealed (155). Stem-inhabiting species (e.g., *Spalacopsis*, *Hippopsis*) are frequently much elongated and slender and, when resting flat against the surface of their host plants with their antennae extended forward, are quite inconspicuous. A less slender and flattened twig-infesting species of Japan, *Aulaconotus pachypezoides* Thomson, cuts a groove in the twig the length of its body and lies in it, head downward, with the body closely appressed to the surface (175). Equally remarkable is *Pharsalia saperdoides* Pascoe of

Borneo, which grasps a twig with its front and middle legs and banded antennae; with its body slanting outward and its hind legs drawn in, it resembles a small, dry branchlet (164).

Bright and contrasting coloration.—In marked contrast to the nocturnal Cerambycidae, diurnal forms are generally brilliantly colored, although Paulian states that some shiny metallic Callichromini are strictly nocturnal (131). Among the sun-loving Cerambycinae, most of the Callidiini are metallic blues or greens (as are many Buprestidae with similar habits), the Clytini are brightly and contrastingly colored, and the Stenaspini exhibit a variety of brilliant and resplendent hues. Other groups have bottle-brush-like tufts of hairs on the antennae or legs, the adaptive significance of which is not clear (12). The flower-visiting species of Lepturini and Clytini are commonly marked with yellow and black, corresponding to prevalent flower colors, particularly in the Compositae, as are the North American species of *Crossidius* (211). Perhaps the most striking of these are the bright yellow, pollinose "pollen-beetles" of México (*Ochraethes*) (61). Other diurnal species, the long-legged Indomalasian *Gerania bosci* (Fabricius), for example, have a yellow bloom to the pubescence which disappears in the dead specimen [Gressitt (*in litt.*)].

Among the exceptions to the generally cryptic coloration of the Lamiinae are certain groups with iridescent or metallic structural colors (309), including the species of *Phacellus*, with patches of refractory scales like those of *Morpho* butterflies. In the Tragocephalini and Sternotomini, groups chiefly confined to tropical Africa, nearly all the species are brightly or contrastingly colored (193, 194), and a great many of them are variable. Numerous "varieties," "geographic races," and "aberrations" have been named. The adults are diurnal and fly during the sunny hours of the day but rest on bushes and trees in the afternoon. Similarly, the diurnal *Zygrita diva* Thomson of New Guinea varies from nearly black to red with a wide variety of spotting, banding, and striping [Gressitt (*in litt.*)], as does the Mexican *Essostrutha fimbriolata* Bates [F. Lane (*in litt.*)]. Whether they are distasteful, and thus warningly colored as are the bright red asclepiad-feeding *Tetraopes* of North America (160), remains to be determined. Even *Tetraopes* may not, however, be universally avoided by birds; Robertson (273) states that *Asclepias* plants in his yard were freed of them by the rose-breasted grosbeak and Forbes (116) reported occasional specimens in blue-bird stomachs. Among the Prioninae, nocturnal habits and somber coloration are the rule, but a few tropical forms are diurnal and brightly colored (e.g., the Central and South American *Pyrodes* and *Psalidognathus s. str.*) (14). Some species are sexually dichromatic in this regard (most of the Neotropical species of *Meroscelisus* are dull colored in both sexes, but the male of *M. violaceus* Serville has bright, metallic blue elytra) (179), suggesting a difference in the diurnal activity pattern of male and female. By contrast, among the West Indian *Elateropsis* the males are dull and the females often have bands of white pubescence; in the Neotropical *Pyrodes*,

the females are often brilliantly metallic, whereas the males are dull bronze.

Batesian mimicry.—Batesian mimicry, involving departures in form and behavior as well as coloration coinciding with those of such hymenopterous models as ants, bees, or wasps, or beetle models as lycids, cantharids, or chrysomelids, is widespread among the diurnal Cerambycidae, especially in the tropics, and exhibits varying degrees of complexity. Unfortunately, few ecologists have carried out the necessary field studies to permit the proper interpretation of the individual cases occurring locally in a given region. Among the earliest contributions to the subject are those of Bates (13) in the Amazon region; the most extensive information was provided by Shelford (291) in Borneo. Gahan (124) and Linsley (213) also have commented extensively on the subject. Shelford's studies are notable as an intensive analysis of the fauna of a small area 20 miles in diameter in which he encountered more than 70 species of mimetic Cerambycidae. No similar study has been made, to my knowledge, in any other comparable area, nor have Shelford's interpretations been confirmed by re-investigation. Nevertheless, his general conclusions appear to be valid, although details may be subject to later revision.

In its simplest form, Batesian mimicry among the Cerambycidae is expressed as "group mimicry," in which the species in a genus, in related genera, or in a tribe have a general but nonspecific resemblance to those of some other group of insects. Thus, the almost universally flower-visiting Lepturinae exhibit certain group characteristics commonly associated with this habit, (e.g., an elongate and attenuated body form and bright coloration). The same characteristics are common among flower-visiting wasps, and selection for wasplike flight and behavior has occurred repeatedly among Lepturinae in many parts of the world. The Clytini, also group mimics of wasps, generally have short antennae, long legs, and yellow and black coloration. These have been selected for wasplike mannerisms in running about over logs and branches in the sunlight. The closely related Tillomorphini, basically clytine in form, consists of species smaller in size. The genera in this tribe are group mimics of ants and usually exhibit a slight constriction of the elytra at the middle, often accentuated by a transverse ivorylike band or an oblique pubescent line, as well as a swollen, convex, pubescent elytral apex, and different coloration before and after the median constriction. This type of group mimicry, although apparently similar in origin to that of the Lepturinae and Clytini, involves some morphological departure from the ancestral type and is often perfected for models of diverse types (307); it may even vary geographically to coincide with geographical color variation in the model (210). Among other sets of group mimics may be mentioned the broad, flattened, sedentary Pteroplatini, which are mimics of specific lycid beetles throughout tropical America; the ovoid, apterous Parmenini, which resemble spiders in both hemispheres; and the Rhyncophora-like Mesosini and Apomycini of the Old World. The Necydalini, on the other hand, are elongated, with short antennae and abbreviated elytra which ex-

pose the flying wings on the abdomen, and are group mimics of Hymenoptera, including not only wasps and bees but also parasitic forms. Such cerambycids are chosen for wasplike behavior only if they are diurnal in habit. Thus, the small, diurnal *Molorchus* exhibit wasplike mannerisms, but not the similarly formed nocturnal *Methia*. In the Methiini, only the diurnal *Coleomethia evaniiformis* Knull (172) is mimetic, adopting the behavior of an evaniid wasp.

Among the Lamiinae there are scattered ant mimics which run rapidly and seldom take flight (94), and many of these are wingless (185). On the other hand, the African genus *Neonitocris* (36) contains species which mimic ichneumonids, braconids, and vespids (124). Lycid mimics reappear numerous times in the Cerambycinae, Lepturinae, and Lamiinae (14, 71, 124, 182, 193, 291), and the Brazilian *Sternacanthus undatus* (Olivier) resembles *Erotylus sexfasciatus* Fabricius. Further, the Burmese *Estigmenida variabilis* Gahan mimics the hispid *Estigmena chinensis* Hope, the Malayan *Ixais castelnaudi* (Thomson), the weevil *Episomus chlorostigma* Wiedemann, and members of the Philippine genus *Dolioops*, weevils of the genus *Pachyrrhynchus*. In South America, various genera, including the remarkable *Zelliboria* also resemble hispids (181), *Ites*, cassidids (182), and *Probatius choliniformis* Lane, the weevil, *Naedius elegans* Lane & Moure (183). On the other hand, *Compsosoma mutillarium* Klug, together with the similarly hairy and brightly colored weevil *Cyphus myrmosarius* Perty, are striking mimics of a mutillid wasp [F. Lane (*in litt.*)]. In Australia, the excessively slender species of *Lygesis* (307) resemble coreids of the genus *Leptocoris*a, and the remarkable Brazilian *Meltzerella lutzi* Costa Lima (69) is marked and colored like a pyrhocorid or reduviid.

Sexual dimorphism in mimicry occurs in the prionine genus *Anacolus*, in which the males resemble wasps and the females mimic *Chauliognathus* and other cantharids.

From the ecological and evolutionary standpoint one of the most interesting groups of Batesian mimics is the Neotropical Rhinotragini. In this tribe, closely related forms resemble, associate with, and behave like groups of insects which are very diverse in form, coloration, and habits. In fact, most of the genera consist of species which are quite obviously mimetic. Some closely resemble protected groups of beetles, as *Chauliognathus* and other cantharids; others mimic and congregate with lycids or resemble hispid leaf beetles. Genera closely allied to these contain flower-visiting species which are vespiform, and the resemblance of such groups to their individual models in flight behavior is very close (13). Rhinotragini also resemble parasitic Hymenoptera and even mosquitoes. Finally, several groups mimic bees, especially those of the genera *Melipona* and *Megachile* (13). Similar, but less diverse, groups of closely related mimics occur in other sections of the family (213, 291).

Müllerian mimicry.—In the West Indies, a "Müllerian ring" of synapostomatic mimicry involving distasteful or inedible forms of various insect

groups, particularly the Coleoptera and Hemiptera, has been investigated by Darlington (81). Included are lycids (*Thonalmus*) colored bright orange or red with the apex of the elytra blue, which are presumed to be models for numerous Batesian mimics, including cerambycids. In a series of experiments, Darlington attempted to determine the relative edibility of some of these Cerambycidae by means of the lizard, *Anolis sagrei* (Duméril & Bibron). In no case did the lizards eat or show any interest in the *Thonalmus*-like species, although they did eat 11 plainly colored specimens of six rather diverse species (some Cerambycinae, some Lamiinae).

Although experimental evidence is accumulating indicating that bees, wasps, and beetles of the families referred to above are generally avoided by vertebrate predators or have a certain degree of immunity from attack [see especially Shelford (291), Jones (160), and Darlington (81)], it appears significant that bee and wasp mimics of the Cerambycidae are generally flower-frequenting types, and that lycid, cantharid, chrysomelid, and ant mimics are most commonly found on trees and other vegetation in the same situations as their models. Also, although there is an abundance of species of Cerambycidae, individuals are often rare, and in mimetic forms they are usually exceeded numerically by their models. Most objections to the theory of mimicry have been directed at the mechanism by which the mimetic pattern is produced. Nicholson (242) emphasizes that protective resemblance apparently offers a slight advantage to certain individuals, rather than to the species as a whole, and thus has been brought about by a gradual accumulation of slight changes in the direction of an ultimate mimetic pattern.

Aptery and adaptations for subterranean existence.—The Lamiinae contain the greatest diversity of wingless or flightless forms. Many of these have been grouped by Breuning (35) into two artificial and admittedly polyphylectic groups, the "Parmenini" and "Morimopsini," comprising 86 genera and hundreds of species scattered over the major continents and various island groups. However, wingless or flightless forms occur in various other sections of the Lamiinae (37) and in the Prioninae (179), and to a lesser extent in other subfamilies. The condition is commonly associated with subterranean or nocturnal habits but also develops in windswept insular environments (203) and other habitats, such as the crests of high mountains, where sedentary habits favor preservation of species (e.g., *Schreiteria bruchi* Melzer, attached to the peculiar *Azorella yareta* at elevations of 3000 to 4000 m. in the Andean region) (42).

Atrophy of the wings is by far the commonest of the adaptations of adult beetles associated with subterranean (root-feeding) habits. The loss of wings usually involves both sexes in the Lamiinae (35), but only the female among the Lepturinae (for example, Philini, Vesperini, *Apatophysis*) (31). Sometimes the male is larger (as in *Morimus*) (49), or it may be considerably smaller (as in *Moneilema*) (262). In the Prioninae, although both sexes may be apterous (as are the Neotropical *Psalidocoptus*, *Apteroaulus*, *Prionocalus*, *Hypocephalus*), more commonly the female is

wingless or at least flightless. In the Indian *Dorysthenes* and the Neotropical *Hypocephalus armatus* Desmarest, the mandibles are elongate and curve downward from the base; they are more prominent in the male. In the males of *Dorysthenes*, the last segment of the palpi is enlarged and dilated; in the female of *Prionapterus* the palpi of the female are more developed than those of the male. Further, in some of the subterranean species the eyes are reduced in size, sometimes only in the female (e.g., *Meroscelisus*), sometimes in both sexes (e.g., *Hypocephalus*). In males of some of the subterranean Anoplodermini (e.g., *Acanthomigdolus*) the posterior trochanters are prolonged as an extended spine (44).

Perhaps the most extreme case of adult adaptation to burrowing habits is the Brazilian *Hypocephalus armatus* Desmarest. The head is peculiarly shaped, the antennae very short, the prothorax enormous, and the legs adapted for digging (the posterior pair have greatly inflated femora and arched tibia) (5, 129).

Adaptations to root feeding also involve larvae (as in *Vesperus*, *Acmaeops*, *Agapanthia*). The adults of *Vesperus*, for example, lay large numbers of eggs (a thousand or more) in irregular groups on or under surface objects, like stones, at the base of trees or vines, or in openings and crevices. The primary larvae are cylindrical and parallel-sided, with long antennae, three ocelli on each side, and very long abdominal setae. After hatching from the egg, they drop to the ground and work their way down through the soil to their food supply, then molt and develop into a short, compressed, posteriorly enlarged, truncate, blind, scarablike grub (276).

The apterous arboreal *Sciadella saltator* Gressitt (134) is not only one of the smallest species in Micronesia (1.8 to 3.3 mm.), but has the habit of jumping several centimeters when disturbed.

NATURAL MORTALITY

Mortality in cerambycid populations from biotic and physical causes may be high. Although published quantitative data are relatively few, something is known of factors which, in general, operate to control population levels. For example, over a five-year period, Peterson (253) found 25-per-cent mortality of *Saperda calcarata* Say eggs, which he attributed to "infertility, climatic conditions, and other physical causes," and 18 per-cent loss which he attributed to parasites, especially *Iphiaulax* (Braconidae). Mortality of 29 per cent occurred among first- and second-year larvae as a result of "climatic conditions, unsuitable or insufficient food, predators, and excessive sap flow in spring," and further mortality in the third and fourth years was caused by a complex of hymenopterous parasites, and hibernating larvae and pupae by woodpeckers.

Predators and parasites.—Among the most effective natural enemies of the Cerambycidae and other wood-boring beetles are predaceous Coleoptera (114). Species of *Cucujus* feed upon both the adults and the larvae. The same is true of such ostomids as *Tenebroides* and *Temnochila*, and numerous clerids, particularly *Cymatodera*, *Thanasimus*, and *Chariessa*,

have similar habits (33, 62). Elaterids of the genera *Alaus*, *Hemirhipis* and *Stenagostus* also destroy them (98, 114, 131, 281), as do the predaceous larvae of Raphidiidae (Neuroptera), which live under bark and prey upon all kinds of wood-boring larvae.

Among the Hemiptera, ambush bugs of the genus *Phymata* include adult cerambycids in their prey (11), and the reduviid *Arilus cristatus* (Hahn) preys on adult *Megacyllene* in North America (279), while *Margasus afziella* Stål and *Rhinocorus nitidulus* (Fabricius) feed on *Neonitocris princeps* Jordan and *Acrocera conjux* Thomson in Africa (141, 161).

Diptera also include several predatory or parasitic groups which feed upon larval cerambycids, the Asilidae and Rhagionidae in particular. Sarcophagids and tachinids parasitize both adult and larval Cerambycidae (105, 147, 195, 278, 296), but their habits are little known. Duffy (93) has also recorded an unknown phorid parasite of *Anelaphus nanus* (Fabricius).

The role of parasitic Hymenoptera in reducing longicorn populations is also poorly understood. Chittenden (63) has recorded a number of parasites of North American species and Elliot & Morley (103) and Kleine (171) have given long lists of parasites reared from various European Cerambycidae. Most of these are in primitive groups (45). Members of the braconid tribes Xordini and Acaenitini are commonly parasitic on economically important species (236), as are several groups of ichneumonids (80, 274, 312), but their significance has not been evaluated. The nematode, *Bradynema strasseni* Wülker, has been reported as a larval parasite of *Rhagium* (268) and adult beetles are commonly infested with mites and pseudoscorpions (308).

Birds—particularly woodpeckers, creepers, flycatchers, nighthawks, vireos, nuthatches, and warblers—derive a part of their food from adult cerambycids (39, 116). Woodpeckers in particular are especially fond of longicorn larvae (40, 41). The sound of larvae at work is frequently discernible at a distance of several feet and the birds probably locate the borers in this manner. Beal (15) found that the wood-boring larvae (including cerambycids) make up 14 per cent of the diet of the downy woodpecker and 77 per cent of the diet of the three-toed woodpecker. According to Jones (160), an analysis of stomach contents of nearly 2000 North American vireos yielded 48 species of Cerambycidae. Among the reptiles, lizards take a large toll of longicorns. They congregate on fallen logs and branches to which the beetles are being attracted and capture them as they fly in. The stomach of the common fence lizard of California (*Sceloporus*) will often yield a dozen or more specimens of *Neoclytus* or *Xylotrechus*. Bats, also, have been observed to capture longicorns, and examination of bat roosts has revealed elytra of *Prionus*, *Ergates*, and other large night-flying species. Undoubtedly many other insectivorous mammals feed upon longicorns when the opportunity arises.

Man must also be included among the significant vertebrate predators of Cerambycidae. From the time of Pliny, who describes the "cossus," a delicacy highly appreciated by the Romans and now generally believed to

be the larva of *Cerambyx cerdo* Linnaeus (29), writers have recorded the use of cerambycid larvae as human food. Duffy (93) lists 22 species, the larvae of which are eaten in various parts of the world, and other species are referred to by Bodenheimer (29). Most of these are Prioninae and Lamiinae, but a few large Cerambycinae are included. Sometimes they are cooked (22) or specially prepared (257), but more often they are eaten raw. In the New Hebrides, Solomon Islands, and New Guinea, where large prionine larvae are extensively used as food, the populations are kept very low in many places [Gressitt (*in litt.*)]. Adult cerambycids—for example, the Australian *Eurynassa australis* Boisduval—are also eaten occasionally. As might be expected, larvae are used as bait by fresh-water fishermen in various parts of the world (87), and in East China mulberry twigs infested with larval *Ceresium sinicum* White are sold as food for caged birds (132, 175). It is doubtful, though, that these latter types of human predation are important factors in population control.

Diseases.—Apparently little has been recorded of diseases of Cerambycidae. Garman (127) recorded *Beauveria bassiana* (Balsamo) (as *Sporotrichum globuliferum* Spegazzini) from dead adults of *Cyllene robiniae* (Forster) in Kentucky, not recognizing that the fungus attacks living individuals. MacLeod (217) reports the same species from the European *Acanthocinus aedilis* (Linnaeus). Other fungi, supposed to be *Isaria* and *Entomophthora*, have been reported affecting *Phrynetta spinator* Fabricius in Africa and *Saperda carcharias* Linnaeus, respectively, in Europe (93). Crawshay (79) refers to an unidentified disease of the larvae of *Tetropium gabrieli* Weise which developed when they were reared under glass. Beeson (20) also noted a disease, supposed to be caused by a virus, in larvae of *Chelosterna scabrator* (Fabricius), which appeared when they were reared in glass tubes (an associated fungus which developed on the larvae was considered to be secondary), and Hasegawa & Koyama (142a) reported a virus disease associated with *Batocera lineolata* Chevrolat. However, the occurrence of virus diseases in Cerambycidae has not been confirmed.

Physical factors.—Temperature is one of the most obvious limiting factors in the life of cerambycid borers, a fact which often accounts for their ecological distribution within a log (130) and has been used as a control measure for injurious species under both natural (74) and artificial (75) conditions. Thus, the exposure of hickory logs to direct sunlight for a few hours will kill all of the immature stages of *Megacyllene caryae* (Gahan) beneath the exposed bark; and in smaller sticks of mesquite two days' exposure will kill 40 per cent of all stages of *Megacyllene antennatus* (White) to a depth of .5 in., a week's exposure will destroy 75 per cent to a depth of .75 in., and two weeks', 90 per cent to the same depth (75). Graham (130) found a wide range in death temperatures for *Monochamus scutellatus* (Say) ranging from 43°C. to 53°C. (average: 47°C.) for adults and from 45°C. to 50°C. (average: 48°C.) for larvae; he attributes their ability to survive and adapt to new conditions to the exceptional individuals falling outside of the average.

However, among Cerambycidae, as with other insects (228), tolerance for high temperatures is greatly influenced by the relative humidity. Savely (281) found that the highest temperatures tolerable to *Romaleum atomarium* (Drury), *Monochamus titillator* (Fabricius), and *Acanthocinus nodosus* (Fabricius) were 49°, 50°, and 46°C., respectively, when exposed in air with a relative humidity of approximately 10 to 15 per cent. With relative humidity of 100 per cent they could tolerate only temperatures of 44°, 44°, and 43°C., respectively. The explanation offered for this phenomenon was that evaporation of water from a larva in dry air has a cooling effect that undoubtedly lowers the body temperature below that of the surroundings. Of the various larvae which Savely tested, those of *Chrysobothris* sp. (Buprestidae) were most resistant to desiccation, and those of *Dendroides bicolor* Newman (Pyrochroidae) least resistant. The percentage of body weight lost by evaporation from larvae of *R. atomarium*, *M. titillator*, and *A. nodosus* was intermediate between that of *Chrysobothris* and *Dendroides*. These differences in resistance to desiccation are correlated with the conditions of moisture in the logs in which the beetles live. Thus the three Cerambycidae are normally found only where the wood is moist, and the humidity of the air around them is probably always near the saturation point. Furthermore, they are not found in parts of a log where the subcortical temperature is likely to be as high above the air temperature as that in the parts inhabited by *Chrysobothris*.

Dürr (97) made a study of the effect of physical factors on adults of *Hylotrufes bajulus* (Linnaeus) and concluded that adults can live, copulate, and oviposit under extremely variable combinations of constant temperature and relative humidity. They seem to be effected to a greater extent by temperature than by relative humidity. The results obtained at various relative humidities, but at a constant temperature, show no significant variation in the average number of eggs per female, in longevity, or in the percentage of females which oviposited. When a constant humidity and different temperatures were used, however, marked deviations occurred. The effect of temperature is most striking on longevity, number of eggs per female, and the percentage of females which oviposited (females were kept with males constantly). Thus, a relatively cool temperature of 52°F. caused the female to live longer, whereas a fairly high temperature of 98°F. shortened the life of the female considerably. The relatively high temperature (98°F.) caused the female to lay fewer eggs than at room conditions, and the cool temperature (52°F.) wholly prevented oviposition. Possibly copulation was also prevented; none could be observed during the daytime at this temperature.

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