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BIOLOGICAL STUDIES OF BRAZILIAN SCOLYTIDAE AND PLATYPODIDAE (COLEOPTERA). II. THE TRIBE BOTHROSTERNINI

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ABSTRACT

The life histories of four species of Bothrosternini (Sternobothrus sculpturatus, S. bicaudatus, Cnesinus gracilis *and* C. beaveri) *are described and suggestions made concerning the habits of* Bothrosternus lucidus. *All species are twig-borers making biramous galleries in the pith. The larvae of four species feed on the pith, those of* B. lucidus *are probably xylomycetophagous. The evolution of the gallery system in Bothrosternini is discussed. The known families of host plants of Central and South American species of Bothrosternini are tabulated. Only* Pagiocerus frontalis *is known to be of economic importance.*

INTRODUCTION

This paper is based on studies made between September and December 1968 of the Scolytidae and Platypodidae of the forest around the base camp of the RS/RGS Xavantina-Cachimbo expedition to North-East Mato Grosso (12° 49'S, 51° 46'W). The first paper of the series (Beaver, 1972) described the methods used and the forest types in the areas studied. It was concerned with the biology of *Camptocerus* Latreille, a genus in the tribe Scolytini in the subfamily Scolytinae. This paper deals with the biology of some species of the tribe Bothrosternini, a tribe frequently included in the Scolytinae, but now placed in the subfamily Hylesininae (Wood, 1961). The following genera are included in the Bothrosternini: *Bothrosternus* Eichhoff, *Cnesinus* Leconte, *Eupagiocerus* Blandford, *Pagiocerus* Eichhoff and *Sternobothrus* Eggers. The biological information available on these genera is briefly reviewed below. Six species of Bothrosternini were collected: *Sternobothrus sculpturatus* (Blandford), *S. bicaudatus* (Blandford), *Bothrosternus lucidus* Wood, *Cnesinus gracilis* Blandford, *C. beaveri* Wood and *Pagiocerus frontalis* (F.).

It may be noted here that Blandford (1896) reversed the sexes in his descriptions of *S. sculpturatus* and *S. bicaudatus*. Dissection shows that it is the female that has dense reddish-yellow pubescence in the depressions on the rostrum and a circular shining area on the frons. In the male, the pubescence on the rostrum is much scantier and the frons duller. The reddish-yellow pubescence on the

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female's rostrum seems to be characteristic of the genus. This suggests that the sexes have been reversed in the description of *S. opaculus* Schedl, and that the descriptions of *S. carinatus* Eggers, *S. rufonitidus* Schedl, *S. suturalis* Eggers and *S. tuberculatus* Eggers also refer to females.

Distribution

The Bothrosternini have an almost entirely Neotropical distribution. A single species of *Cnesinus* (*C. strigicollis* Le Conte) is found in the United States (Wood, 1968), while *Pagiocerus frontalis* has been imported into Europe, Russia, U.S.A. and Africa (Schedl, 1965) in maize (*Zea mays* L.). Of the five Bothrosternine genera, only *Eupagiocerus* has not been found in Brazil. It has a Central American distribution. The known range of the species found is given below.

Sternobothrus sculpturatus is known from Argentina, Colombia, Costa Rica, Panama, Venezuela and from the states of Mato Grosso and Santa Catarina in Brazil.

S. bicaudatus is known from Panama, Peru, Venezuela and Brazil (Mato Grosso).

Bothrosternus lucidus is known only from the present study in Brazil (Mato Grosso).

Cnesinus gracilis is recorded from Costa Rica to Panama (Wood, 1968), but has not been found before in Brazil.

C. beaveri is known only from the present study in Brazil (Mato Grosso).

Pagiocerus frontalis is known within the Neotropical region from Argentina, Bolivia, Chile, Colombia, Costa Rica, Cuba, Ecuador, Guadeloupe, Guatemala, Mexico, Panama, Peru, Trinidad, Venezuela and Brazil (Mato Grosso).

Host plants

Most of the information on the host plants of the Bothrosternini comes from the papers of Schedl (1965), Viana (1965) and Wood (1965, 1967, 1968). A few other records are scattered in the literature. The information for the Central and South American species is summarized below:

Host family	Scolytid species attacking
Annonaceae	*P. frontalis* (F.)
Araliaceae	*C. denotatus* Wood
Boraginaceae	*P. frontalis*
Compositae	*C. annectens* Wood
Fagaceae	*C. elegantis* Wood, *C. gibbulus* Wood
Gramineae	*C. guadeloupensis* Eggers, *P. frontalis*
Lauraceae	*C. bicinctus* Schedl, *P. frontalis*, *S. sculpturatus* (Blandford)
Leguminosae	*C. adusticus* Wood, *C. dividuus* Schedl, *C. dryographus* Schedl

Malvaceae	*C. dryographus*
Moraceae	*C. insularis* Eggers
Oleaceae	*C. dividuus*
Rosaceae	*C. carinatus* Wood
Rubiaceae	*C. coffeae* Schedl, *C. foratus* Wood, *C. robai* Blackman, *C. substrigatus* Blackman, *P. frontalis*
Sapindaceae	*C. degener* Wood, *E. ater* Eggers
Sapotaceae	*C. ampliatus* Schedl
Valerianaceae	*C. atrddeclivis* Wood
Tree branches	*C. foratus, C. columbianus* Wood
Tree twigs	*C. electinus* Wood, *C. minitropis* Wood, *C. niger* Wood, *C. perplexus* Wood
Vines	*B. definitus* Wood, *C. degener, C. frontalis* Wood, *C. gibbosus* Wood, *C. myelitis* Wood, *C. retifer* Wood, *C. squamosus* Wood, *E. dentipes* Blandford, *E. vastus* Wood
Herbs	*C. atavus* Wood, *C. bicornus* Wood

With two exceptions, each scolytid species has been recorded from only one species in the plant family indicated. *S. sculpturatus* has been recorded from *Nectandra lanceolata* Nees et Mart. ex Nees (Lauraceae) by Santoro (1957), and from *Nectandra* spp. by Wood (*in litt.*). *P. frontalis,* a spermatophagous species, is recorded from the seeds of five species of Lauraceae, two species of Annonaceae and one of Boraginaceae, as well as from stored maize and coffee beans. Other spermatophagous species are *C. guadeloupensis* Eggers, recorded from maize by Wichmann (1954), and *C. foratus* Wood recorded from coffee berries, but also from dead branches by Wood (1967). Wichmann (1954) records *Cnesinus obscurus* F. from coffee berries, but no species of this name has ever been described and the species in question is uncertain (Schedl, 1962/3). It seems most likely to be an error for *Hypothenemus obscurus* (F.), a species known to attack a wide variety of seeds and fruits, including coffee berries (Costa Lima, 1956, Kalshoven, 1963).

The host records in Table 1 cover a wide range of families, but much more investigation will be required before the real host range of each species is known. It is unlikely that the species are as monophagous or oligophagous as they now appear to be. In most cases in which the size of the host is recorded, the non-spermatophagous species are found to live in small twigs or stems of 2 cm diameter or less. The maximum diameter recorded is 5 cm.

The host records obtained in the present study are summarised in Table 2. The host preferences are relatively restricted. Cut trees and climbers of at least 20 other families in the same area were not attacked. With the exception of the Burseraceae and Rubiaceae, the hosts belong in two orders of plants (Ranales and Rosales) which are probably closely related and which were attractive to quite a large number of scolytid and platypodid species.

S. sculpturatus was found only on trees in the gallery forest, *S. bicaudatus* and *C. beaveri* equally on trees in gallery and valley forests, *B. lucidus* and *C. gracilis* almost entirely on trees in the valley forest. Further data are needed to determine whether these are real habitat preferences or sampling artefacts.

Family	Host tree Species	Local name	No. of trees cut	S.sc	S.bi	B.lu	C.gr	C.be
Annonaceae	Guatteria spp.	Invireira	4		1		1	1
Monimiaceae	Siparuna aff. guianensis	Capitiú	2		2			1
Lauraceae	Ocotea guianensis	Louro dorado	1	1	1			
	?	Louro preciosa	3	1	1			
Rosaceae	Hirtella spp.	Quebra colhão	3		1	1	1	
Leguminosae	Pterodon pubescens	—	2				1	
	(woody climber)	—	2				1	
Burseraceae	Protium spp.	Breu branco, etc.	15		2	3	2	
Rubiaceae	?	Maria molle do brejo	1	1				
?	(liane)	Cipo mucuna	2				1	
		Total	35	3	8	4	7	2

Table 2: Host trees of Bothrosternini in the present study.
(S.sc = *Sternobothrus sculpturatus;* S.bi = *S.bicaudatus;* C.gr = *Cnesinus gracilis;* C.be = *C.beaveri;* B.lu = *Bothrosternus lucidus*)

Th range and mean diameter in cm of the stems sttacked are given below for each species. *S. sculpturatus,* 0.7-2.6: 1.22; *S. bicaudatus,* 0.3-1.2: 0.66; *B. lucidus,* 0.3-0.7: 0.50; *C. gracilis,* 0.2-0.9: 0.44; *C. beaveri,* 0.2-0.4: 0.32. It is clear that all species breed in small twigs or branches. There is considerable overlap between the species in the size of stem attacked, and to some extent the species overlap in the field. In five trees, two species of Bothrosternini were found together, and in two trees (*Hirtella* sp. and *Protium* sp.), three species were found occupying stems of similar diameter. In a further eight trees, only a single species was present. However, the mean stem diameters suggest that there is some ecological separation between species. This separation is related to beetle size. The rank order of mean stem diameters is the same as the rank order of adult beetle diameters.

Only one specimen of *P. frontalis* was obtained, from a light trap at the edge of gallery forest, and the species will therefore not be considered further.

Life Histories

There is little information available on the gallery systems and life histories of Bothrosternini. The gallery systems of three species of *Eupagiocerus* (*E. ater* Eggers, *E. dentipes* Blandford (= *clarus* Wood) and *E. vastus* Wood) are briefly described by Wood (1965). Chamberlin (1939) has a brief note on the gallery of *Cnesinus strigicollis.* The gallery system of *Cnesinus annectens* Wood is described by Wood (1967) and that of *Bothrosternus definitus* Wood by Wood (1968). The biology of the spermatophagous *P. frontalis* (= *fiorii* Eggers) is described by Yust (1957).

In all the twig-inhabiting species except *C. annectens,* the gallery system consists basically of a radial gallery running directly from the surface to the central pith of the stem and extensions from this gallery up and down the stem in the pith. In *C. annectens,* there are biramous parental galleries in the phloem resembling those of *Leperisinus varius* (F.), but the female usually later cuts a tunnel into the pith and along the central axis of the stem (Wood, 1967, and *in litt.*). The larvae of *C. annectens* feed in the phloem at first but then move to the pith and continue feeding there. In *E. vastus* and *E. dentipes,* the larvae also feed on the pith, extending the parental galleries. In *B. definitus* and *E. ater,* a fungal mycelium was found in the galleries, and there seems no doubt that this is an ambrosia fungus fed on by the larvae.

The gallery systems of the species studied resemble the basic type given above. The gallery is started either in a leaf scar or between two nodes. In *Cnesinus* spp. most galleries were started about halfway between two nodes; in *Sternobothrus* spp. this positional preference was not found. The entrance hole leads directly into a radial gallery which usually runs straight through the central pith. (In all stems attacked, a central pith 0.12-0.40 cm in diameter was present.) In *C. beaveri,* the radial gallery has a slight enlargement where it enters the pith, but this is absent in other species. The gallery is then extended, usually both up and down the stem in the pith, but occasionally in one direction only.

The precise form of the longitudinal gallery depends on the diameter of the pith relative to the diameter of the beetle. If both diameters are equal, the whole pith is excavated; if the beetle is smaller, e.g. *Cnesinus* spp., the gallery may be more irregular, sometimes following a spiral course around the edge of the pith. In *C. beaveri,* a third longitudinal branch was found in two gallery systems, starting near the beginning of one longitudinal branch and running through the pith. Occasionally two gallery systems may connect within the twig. The numbers and lengths of galleries examined are given in Table 3 for *Sternobothrus* spp. and *Cnesinus* spp. Only two gallery systems of *B. lucidus* were examined, neither of which contained offspring.

The following details of the life history apply to all species except *B. lucidus.* The gallery system is normally started by the male. He cuts the radial gallery and most, probably all, of the longitudinal galleries. He appears to continue extending the galleries until joined by a female, since some galleries containing only the male were longer than others containing a female and eggs or larvae (Table 3). It is not certain whether there is further extension when female is present; but when both sexes are found in a gallery, the male is usually in the radial gallery, and he may help to protect the gallery system against predators attempting to enter it while the female is laying eggs. After some, perhaps all, the eggs are laid, the male leaves the gallery. Only the female was found in gallery systems with larvae or pupae. The female probably remains in the gallery until about the time that the brood emerges. Wood (*in litt.*) notes that in some species of *Cnesinus,* a female may construct a gallery system and rear a brood without a male being present. These may be second or later broods produced without the need for more than one mating. The possibility of this cannot be ruled out here, since some galleries did not contain males

	S. sculpturatus	*S. bicaudatus*	*C. gracilis*	*C. beaveri*
Total no. of galleries examined	10	17	23	6
Length of longitudinal galleries without eggs (range and mean in cm)	1.7-14.2/6.4	0.4-2.1/1.0	0.3-2.6/1.0	0.2-0.9/0.5
Length of longitudinal galleries with eggs (range and mean in cm)	1.1-5.6/2.6	1.0-2.0/1.5	1.6-4.3/2.8	0.8-1.4/1.2
Length of longitudinal galleries including larval galleries (range and mean in cm)	5.1-12.6/9.1	7.8-12.0/9.9	1.9-5.8/4.1	1.6-3.2/2.4
Maximum and mean no. of offspring per gallery system	10/7.0	9/5.3	8/5.0	9/3.8

Table 3: Data on gallery systems of four species of Bothrosternini.

The eggs are laid in separate niches in the walls of the longitudinal gallery, usually towards the ends. Each egg is packed into the niche with frass. The number of eggs laid by a female in a gallery seems to be very small (Table 3). The calculations of the average number of offspring per gallery may have included some galleries in which oviposition was incomplete, but the maximum numbers of offspring found are also low. This suggests that a female can produce more than one brood. The larvae of *Sternobothrus* and *Cnesinus* found in this study feed largely or entirely on the pith and no fungal growth was noted in the galleries. On hatching, the larvae make rather irregular galleries through the pith. These never penetrate the wood. When the maternal gallery occupies almost the whole of the pith, the larval galleries extend beyond it; when there is more pith left, the larval galleries may run in a similar way or towards the radial gallery. As the larvae of *Sternobothrus* spp. and *C. gracilis* grow most of the pith is eaten away and the cavity produced becomes filled with frass together with much of the parental gallery. It is often impossible to determine where the parental gallery ends and the larval galleries begin. The average length of the larval galleries may be determined approximately from Table 3 as the difference between the mean length of galleries including larval galleries and the mean length of galleries with eggs. The mature larvae may be found in the frass or in the pith. *C. beaveri* is a very small species, and the larvae do not usually excavate the whole of the pith. In this species, the parental gallery did not become frass-filled.

B. lucidus is almost certainly a xylomycetophagous species. *Bothrosternus* spp. are characterised by a pleural tuft of setae on the prothorax (Eggers, 1943), and species with this character are associated with ambrosial fungi (Wood, 1965). Unfortunately, no fully developed gallery systems of this species were found.

The mature larvae of *Sternobothrus* spp. pupate in cells cut in the pith at the edge of the extended gallery system. Pupae of *Cnesinus* were not found. The adults of the new generation emerge through the entrance hole cut by the parent.

No parasites or predators of the immature stages were found.

The time required for the development of the immature stages is not known accurately. There is evidence that attacks on the stems continued over a long period after they were cut. Galleries containing a single male or a male and female without offspring or with unhatched eggs were found 70-80 days after felling. In addition, the time between the initial attack and the start of egg-laying is not known. For these reasons only the minimum developmental times are given. Medium-sized larvae of *S. sculpturatus. C. gracilis* and *C. beaveri* were found 17-24 days after attacks started. Pupae were present after 37 days in *S. bicaudatus* and after 46 days in *S. sculpturatus,* while adults of *B. lucidus* emerged after 43-49 days. The larvae or pupae in one gallery system were usually at about the same stage of development. This suggests that the eggs are laid over a fairly short period of time (a few days).

Associated species

A total of 25 species of Scolytidae and 2 species of Platypodidae were found in the same trees as the five species of Bothrosternini.

Of these, only two species of Scolytidae (*Xyleborus splendidus* Schaufuss and *Microcorthylus* sp. 2) occurred as many as four times. Both of these species were fairly widely distributed in other trees and attacked larger sized branches than the Bothrosternini. Of the species occurring three times, three are of interest: *Camptocerus aquilus* Wood, *Periocryphalus sobrinus* Wood and *Cryptocarenus heveae* Hagedorn. These species and the Bothrosternini attacked twigs of similar diameter and are potential competitors.

Economic importance

None of the Bothrosternini seems likely to be of economic importance as timber pests. They breed almost entirely in small twigs and stems and do not attack large timber. In addition, the species studied are clearly secondary species, only attacking dying and dead twigs, often a considerable time after the trees were felled. However, other species may be more aggressive and could injure young trees. A number of twig-boring species of Scolytidae are pests, and Browne (1961) considers that any twig borer should be considered a potential pest until its harmlessness has been demonstrated. *P. frontalis* has potential importance as a pest of stored maize (Wichmann, 1954, Schedl, 1965), but serious damage appears to have been reported only in Ecuador (Yust, 1957).

Discussion

Based on the limited present knowledge of the biology of the Bothrosternini, it is possible to suggest an evolutionary sequence in the form of the gallery system. It is suggested that the group evolved from phloeophagous ancestors in which the parental gallery was made between the phloem and xylem of small branches, and the larvae fed together in a group in the phloem. The next stage is represented by *C. annectens* (Wood, 1967). The eggs are laid in a gallery cut in the cambial region, but the female also cuts a tunnel into and along the pith. The larvae feed at first in the phloem but after second instar move into the pith. In the next stage, the cambial gallery is lost. The eggs are now laid in the longitudinal gallery in the pith and the larvae feed on the pith. This stage is represented by *S. sculpturatus, S. bicaudatus, C. gracilis* and *C. beaveri* (see above), and by *E. dentipes* and *E. vastus* (Wood, 1965). In the final stage, there is a transition from a pith-eating to a fungus-eating habit. This stage and probably also the earlier ones must have occurred at least twice, since examples are found in the genera *Bothrosternus* and *Eupagiocerus* (Wood, 1965, 1968). The larvae no longer make galleries in the pith, but feed on the ambrosia fungus growing on the walls of the parental galleries (*Eupagiocerus*) or in cells in the pith (*Bothrosternus*). At some stage or stages in the above series, certain species (e.g. *P. frontalis*) have become spermatophagous.

In *Bothrosternus*, as in many xylomycetophagous Scolytidae (e. g. the tribes Xyleborini, Webbini (Browne, 1961)), there seems to be a reduction in the number of males produced relative to

females. In the Xyleborini and Webbini, this is associated with considerable sexual dimorphism. The male never leaves the parent gallery and mating occurs before the female offspring emerge from the gallery. In almost all *Bothrosternus* species, sexual differences are no greater than in related genera, but it is possible that mating occurs within the parent gallery and that gallery construction is by the female rather than the male. Gallery construction by the female has been noted above in certain *Cnesinus* species.

Scolytid species (e. g. most Bothrosternini) living in and feeding on the pith of twigs are usually classified as xylophagous (e. g. Browne, 1961). However, so far as the scolytids are concerned, it seems likely that the pith resembles more closely in structure and food content the soft tissues of herbaceous plants rather than the hard woody tissues fed on by truly xylophagous beetles, e. g. Bostrychidae, Anobiidae. The occurrence of two species of *Cnesinus* in herbs (Table 1) is therefore of interest. Few species of Scolytidae are known to be herbiphagous (Schedl, 1958, Browne, 1961). Since non-woody stems are almost invariably of small diameter, it seems likely that the herbiphagous habit evolved from the more widespread twig-infesting and pith-feeding habit.

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ADDENDUM

In a recent paper, Wood (1971, *Great Basin Nat. 31*: 140-152) synonymises *Cnesinus substrigatus* Blackman with *C. gracilis* Blandford. The distribution of *C. gracilis* therefore extends to Colombia, and its hosts include *Coffea arabica* L. (Rubiaceae).