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A review of the literature on the life history of Bostrichidae
(Coleoptera)

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Abstract

We review the scattered published literature in many languages on the biology of the beetles family Bostrichidae, and discuss it according to the type of breeding place (stored cereals, dead wood and timber, living tree) in which the bostrichids become pests. We summarize the available data in three life history tables.

Introduction

Bostrichids are commonly known as powder-post beetles, because of the ability of the larvae to reduce sapwood, particularly of hardwoods, into a powdery frass. Hence, the beetles are of considerable economic importance to forestry and the wood-using industries (RAI & CHATTERJEE 1963), and a few species have become important pests of timber, wooden works and ancient structures in tropical countries (HICKIN 1975).

Except for the economically important species, such as the important pests of cereals (FISHER 1950, CABI 2008), *Rhyzopertha dominica* (FABRICIUS, 1792) and *Prostephanus truncatus* (HORN, 1878), and the important pests of wooden and bamboo structures (FISHER 1950; GERBERG 1957), *Sinoxylon* spp., *Dinoderus* spp. and *Lyctus* spp., studies of the life history of Bostrichidae have rarely been made, because the propensity of the Bostrichidae to burrow into sapwood made the task of studying the life-cycle very difficult (RAI & CHATTERJEE 1963).

Compared to other Polyphagan beetles, we know far too little about the biology of the xylophagous ones, especially the Bostrichidae (MATEU 1967). Hence, we have tried to review as many references about the biology of Bostrichidae as we have been able to collect. These references are scattered in different journals throughout the world, and in many different languages. We hope this paper can provide the basic knowledge about the biology of Bostrichidae to encourage more people to study the family further.

Host Plant

Bostrichidae are among those beetles which seem most perfectly adapted to a xylophagous way of life (LESNE 1924). Both as adults and larvae they feed on the woody tissues of their host plants. Most species gain their food from starches and sugars in the plant tissues on which they feed, but endosymbiosis with bacteria in mycetomes of the hind part of the midgut is well-known in Bostrichidae (CROWSON, 1981).

Bostrichids are almost never confined to particular host plants (LESNE 1911). BEESON and BHATIA (1937) recorded about 42 families, 145 genera, 226 species of plant hosts in India, amongst which Caesalipiniaceae, Mimosaceae, Papilionaceae, Anacardiaceae, Euphorbiaceae and Dipterocarpaceae were the most 'popular' host plant families. Some species can develop in quite different types of food, e.g. *Heterobostrychus brunneus* MURRAY and *Dinoderus minutus* (FABRICIUS) develop side by side both in bamboo, and in dried potato tubers (LESNE 1911).

Only *Endecatomus* LECONTE 1861 has been reported to feed on fungi, *Polyporus* spp., growing on the dead logs of birch (*Betula*) (CROWSON 1961; KOMPANTSEV 1978). The biggest bostrichids, *Dinapate wrighti* HORN (over 30mm long) is the only palm feeder in Bostrichidae. It feeds on the California endemic fan Palm, *Washingtonia filifera*, and other species of this genus (GARNETT 1922).

Although most bostrichids are not host-specific, and are often strongly polyphagous, some show preferences for particular hosts, e.g. some species of *Dinoderus* STEPHENS 1830 normally breed only in bamboos (BEESON & BHATIA 1937). The palearctic genus *Stephanopachys* WATERHOUSE is unusual in breeding only in coniferous trees. The main hosts of *Stephanopachys* are *Picea* spp., *Pinus* spp. and *Abies* spp. in Europe, *Pinus sylvestris* and *Larix gmelinii* in North China (ZHANG & CHU 1995). *Stephanopachys* is the only genus of Bostrichidae specialized to feed on gymnosperms, and is the only exclusively phloeophagous genus among the bostrichids (LESNE 1911).
Partly because of the wide range of host plants, bostrichids can become important economic pests of stored cereals, dead woods or wooden products, and occasionally even of living trees. Here we review the literature of the life history of bostrichids according to the type of host in which they become pests.

Stored Cereals Pests

The larger grain borer, *Prostephanus truncatus* and the lesser grain borer, *Rhyzopertha dominica* are most important pests of stored cereals, so their life histories have been studied most in the Bostrichidae (e.g. RAO 1969; BEGUM & HUDA 1974; GUNTRIP et al. 1997; BORGEMEISTER et al. 1998; NANSEN & MEIKLE 2002; CHANDER & BHARGAVA 2006) .

A relationship between stored product insects and storage fungi in stored grain ecosystems is often present and complex (ABDEL-KAWY & YOUNIS 1998). *Prostephanus truncatus* hosts both extracellular and intracellular symbiotic micro-organisms. The symbiotic extracellular bacteria are embedded in a microfilm in the ileum. The microfilm is developed by the host and suggests a co-evolutionary relationship between *P. truncatus* and the extracelluar bacteria (NANSEN & MEIKLE 2002). The female *P. truncatus* frequently have larger endo-symbiotic bacteriomes than the males and this is probably attributable to the higher nutritional requirements of females (NANSEN & MEIKLE 2002).

The male *P. truncatus* produces a pheromone which attracts females to his tunnel, then the female produces certain chemical compounds which suppress the male pheromone so that only a single female is attracted (NANSEN & MEIKLE 2002). There are three steps in the courtship behavior of *P. truncatus*: (1) ushing by both sexes, but mainly females, during a pre-copulatory period; (2) after mutual acceptance, rubbing of the female at the base of the elytra by the male using his antenna and legs; (3) the male climbs on the back of the female. Copulation then follows. Pairs were observed to copulate repeatedly over a period of several days (NANSEN & MEIKLE 2002).

P. truncatus has a potential adult life span of at least two months and the females lay eggs in small clutches, usually in 'blind' side-tunnels to the main tunnel, and each egg clutch is usually protected by tightly packed frass (NANSEN & MEIKLE 2002). They feed chiefly on stored dried maize, cassava, sweet potato (GUNTRIP et al. 1997) and are described as 'internally feeding' insects because the females oviposit inside the host and the entire egg to emergence cycle is completed within the same host (NANSEN & MEIKLE 2002). The larval development of *P. truncatus* is sensitive to moisture content, while egg and pupal development is unaffected by the moisture content. The development time from egg to adult at 70% RH ranges from about 25 days at 32 ˚C to 167 days at 18 ˚C. The hatching of eggs takes 4-14 days, three larval instars are completed in 16 - 129 days, and the pupal stage can last for 5 - 25 days (NANSEN & MEIKLE 2002, see also table 1).

Rhyzopertha dominica feeds on stored grains and similar starchy products and damages all kinds of stored grains and a wide variety of foods (RAO 1969; BEGUM & HUDA 1974). The adult female deposits eggs in clusters of 2 to about 30, and one female can lay from 200 to 500 white eggs during a lifetime (BEGUM & HUDA 1974). The eggs are laid on the outside of the grain or in the fine powdered grain associated with infestations of this beetle (RAO 1969). There are four larval stages. Development times from egg to adult depend on temperature. The life cycle may take fewer than 30 days in the hot summer, but the average is about 58 days (BEGUM & HUDA 1974, see also table 1). Both the larvae and adults produce a large amount of frass or waste (RAO 1969).

Tab1. Life cycles of the stored cereals pests**.**

Species	The duration of development (days)				
	Requirements	eggs	larvae	pupae	adult
Prostephanus truncatus (HORN) [1]	70%RH, 32 ˚C	4	16	5	>60
	70%RH 18 ˚C	14	129	25	60
Rhyzopertha dominica (FABRICIUS) [2]	average	58			>30

[1] NANSEN & MEIKLE 2002; [2] BEGUM & HUDA 1974

Forest and Wood Pests

The life histories of some of the forest and wood pests have been studied or reviewed from time to time, such as *Lyctus* spp. (SNYDER 1916, FISHER 1929, PARKIN 1934, CHRISTIAN 1940, GERBERG 1957, ROSEL 1969, IWATA & NISHIMOTO 1985), *Dinoderus* spp. (BEESEN & BHATIA 1937, LIU 1956, CHANG et al. 1979) and *Sinoxylon* spp. (RAI & CHATTERJEE 1963). LESNE (1924) mentioned that the bostrichid adults are very active during the period after their emergence. The great majority of Bostrichidae are nocturnal and frequently attracted to light in the evening.

There are few references to the courtship and mating activity of the forest and wood pests. Sometimes the males are involved in pre-mating aggression towards each other prior to courtship and mating (LESNE 1924). They struggle thorax against thorax, the mandibles open, seeking to sever the antennae of the opponent. One of them may slide its prothorax beneath the abdomen of its rival, then rising sharply, makes it lose its footing and throws it into space. When a male meets a female, using the palps and antennae, it explores the elytral declivity, then drums on the same area with its tarsi, sometimes the anterior tarsi, sometimes the posterior (LESNE 1924).

The position of the male relative to the female during mating depends primarily on the general body form, and whether it is short and thick or the opposite. Among the lyctines, in which the body is depressed, mating occurs with the male above the female. In the bostrichines, which have a cylindrical and hence very convex form, the bodies of the male and female face in opposite directions after the beginning of mating (LESNE 1924).

Adult lyctines are sexually mature upon emergence. Copulation occurs soon afterwards, more often at dusk or nocturnally than diurnally. Oviposition takes place 2 to 3 days after mating, usually nocturnally. The female may feed on the surface of the wood by gnawing the torn fibers, possibly to detect the suitability of the timber for oviposition in relation to food value for the larvae (GERBERG 1957).

The females laid the most eggs within the first 7 to 8 days of their adult life (GERBERG 1957). The egg-laying period usually lasts from two to twelve days at 26 ˚C (PARKIN 1934) and from 19 to 20 days at 15 ˚C (CHRISTIAN 1940, see also table 2). The larva usually follows the grain of the wood at first, but it does not always confine its initial tunnel to the pore in which it was born. It may at once bore into the tissues at an angle to this pore (FISHER 1929).

The larvae of *Lyctus* feed mainly on the sapwood of hardwoods, and the chief source of food of the larva is the starch in the cell content of the wood. Beside starch, certain sugars, disaccharides, and a polysaccharide, as well as protein, are necessary constituents of the larval food. Moisture is also essential for the normal development of the larva. It will thrive in wood with a moisture content of between 8 and 30 percent. In this range, the higher the moisture content, the more favorable to larval growth (GERBERG 1957).

The larval stages last from four to ten months under natural conditions, although the period can be shorter as the temperature increases (CHRISTIAN 1940, FISHER 1929), and the winter is passed in the larval stage (FISHER 1929). The numbers of instars of *Lyctus brunneus* (STEPHENS, 1830) is usually four under the natural conditions, but can increase to eleven in laboratory conditions with an insufficient supply of food, but the surviving larvae die after eleventh instars (IWATA & NISHIMOTO 1895). When fully grown,

Tab 2. Life cycles of the forest and wood pests.

Species	The duration of development (days)				
	Requirements	Egg	larva	pupa	adult
Lyctus spp.	tropical area[1]	8-12	about 120	12	>30
	temperate area[2]	19-20	about 300	30	>30
Dinoderus minutus	tropical area[3]	<7 generations per year			
Dinoderus japonicus	temperate area[4]	one generation per year			
Dinoderus ocellaris	tropical area[3]	3-4 generations per year			
Sinoxylon anale[3]		3 months to four years per generation			
Sinoxylon crassum[5]		-	-	8-17	-
	warmest area in India[3]	4 generations per year			
Polycaon chilensis[6]	in Argentina	12-21	630-720	14-22	60

[1] PARKIN 1934, FISHER 1929; [2] CHRISTIAN 1940, GERBERG 1957; [3] BEESON & BHATIA 1937; [4] LIU 1956, CHANG et al. 1979 ; [5] RAI & CHATTERJEE 1963; [6] SOLERVICENS & VIVAR 1976

Lyctus larvae tunnel towards the surface of the wood, and within a short distance of the surface, excavate an oval pupal chamber in which pupation takes place. The pupal period lasted from twelve days in tropical areas to one month in temperate areas (FISHER 1929, GERBERG 1957, see also table 2).

BEESON and BHATIA (1937) reviewed extensive studies on *Dinoderus* in their paper on the biology of Bostrichidae. In the tropics, *Dinoderus minutus* can breed throughout the year and the maximum number of the generations is about seven (BEESON & BHATIA 1937). The life-history of *Dinoderus brevis* (HORN, 1878) is stated to be very similar to *Dinoderus minutus*, but *Dinoderus ocellaris* STEPHENS, 1830 hibernates as an egg and three or four generation in the year in north India and five generations in the year in Bengal (BEESON & BHATIA 1937, see also table 2). In the temperate climate, *D. minutus* and *Dinoderus japonicus* LESNE, 1895 mostly have an annual life cycle and pass the winter as adults, but a small proportion of the adults emerge in July and produce a second but incomplete generation which passes the winter as larvae (LIU 1956, CHANG et al. 1979).

In the case of *Sinoxylon* spp. as pests of wood, BEESON and BHATIA(1937) mentioned the quickest possible rate of development of *Sinoxylon crassum* LESNE 1897 might be a series of four generations in one year in the warmest parts of India, and the pupal period ranges from 8 to 17 days (RAI & CHATTERJEE 1963). The life-cycle of *Sinoxylon anale* LESNE 1897 is about three months at a minimum and the maximum recorded at Dehra Dun is more than four years (BEESON & BHATIA 1937, see also table 2). *S. anale* emerges throughout the year, and no regular sequence of generations nor regular correlation between the length of the life-cycle and the season of the year is found (BEESON & BHATIA 1937).

In Argentina, *Polycaon chilensis* (ERICHSON, 1834) often attacks the dead trunks or branches of eucalyptus (*Eucalyptus globulus*) and other broadleaved trees. The adults of *P. chilensis* emerged in the southern summer from the end of October to the end of March and the adult stage usually lasted for 60 days. The eggs took 12 to 21 days to incubate in the months from December to February. The larva has four instars and spent 630 to 720 days in the wood developing their galleries before they pupated. The pupal stage only lasted 14 to 21 days between October and January (SOLERVICENS & VIVAR 1976, see also table 2).

In the northwest Sahara, *Xylomedes rufocoronata* (FAIRMAIRE 1892) attacked the dried branches and twigs of *Rhus tripartitus* and *Retama retam*, both of which are common in the region (MATEU 1967). MATEU (1967) found the adults of *X. rufocoronata* emerged during the spring from April to May whether from artificial cages or in natural conditions. In Spanish Sahara, *X. rufocoronata* emerged from February to May, and until October in Somalia and Ethiopia (MATEU 1967).

Tab 3. Life cycles of reported living tree pests.

Species	Location	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Sinoxylon perforans [1]	Pisa, Italy				o o o o o o								
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							+ + + + + +						
		* * * * * * * * * * * * * * * * * *						* * * * * * * * * * * * * * * * * *					
Sinoxylon japonicum [2]	Loyang, China				o o o o o o o								
						- - - - - - -							
							+ + +						
		* * * * * * * * * * * * * * * *						* * * * * * * * * * * * * * * * * * * *					

* o: egg, -: larva, +: pupa, *: adult [1] FREDIANI 1961; [2] ZHAO & HO 2000

Pests of Living Trees

There are few examples of Bostrichidae attacking living trees and breeding there. However, there are more records of damage caused by young adults tunnelling in young stems and shoots to feed before breeding elsewhere (so called 'maturation feeding', see below). FREDIANI (1961) studied *Sinoxylon perforans* (SCHRANK, 1789) which was found attacking vines, wild cherry and pear trees around Pisa in autumn 1957. In Pisa, *S. perforans* took one year to complete the life cycle and passed the winter as adults. It took two months (April and May) from eggs to larvae, the larval period took about three months (the end of May to the beginning of August), pupae were found from the end of June to the middle of August, and the adults emerged from July, with overwintering adults emerging up to the middle of the following June (FREDIANI1961, see also table 3).

Sinoxylon japonicum LESNE, 1895 has been found attack two to three years old young flamegold trees (*Koelreuteria integrifolia*) in Loyang, China (ZHAO & HO 2000). From the middle of March to the end of May, the adults of *S. japonicum* usually wandered along the branches during the day time to mate. After mating, the female returned to the gallery from which it came to keep boring and ovipositing (ZHAO & HO 2000). *S. japonicum* completed its life cycle in one year in Loyang and passed the winter in the adult stage. The adult oviposits from the middle of March to the middle of May, the larvae were present from the end of March and pupated from the end of May. The adults emerged from the beginning of June and prepared to pass winter from the end of October (ZHAO & HO 2000, see also table 3).

Damage caused by the maturation feeding of bostrichids in young stems and shoots of living trees can result in dieback, increases the risk of breakage by wind and infection by pathogens. This can be important if the trees attacked are of economic value. Such feeding and resultant damage has been recorded in species of the bostrichid genera *Apate* FABRICIUS, 1775 and *Botrychopsis* LESNE, 1899 in Africa (BROWNE 1968, WAGNER et al. 1991), and *Sinoxylon* DUFTSCHMIDT, 1825 in India and Southern Africa (BROWNE 1968).

Conclusion

This review shows that more effort is needed to study the biology of Bostrichidae, especially the pests of living trees. The life cycles, courtship and mating activity, the galleries of different species, as well as the relationship between Bostrichidae and both extracellular and intracellular symbiotic micro-organisms that are supposed to be involved in the nutrition of the beetles are all worth further studies and will probably reveal information to the phylogeny and evolution of Bostrichidae.

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Zusammenfassung

In der vorliegenden Arbeit wird ein Überblick zur Kenntnis der Biologie der Käfer der Familie Bostrichidae gegeben. Besonders berücksichtigt weren dabei die verschiedenen Holzarten, die die Bostrichiden bewohnen: Getreidespeicher, totes Holz und Bauholz, lebende Bäume. Die Informationen über den Lebenszyklus von Bostrichiden wurden in Tabellen zusammengefasst. Es wurden alle erreichbaren, teils sehr verstreuten Publikationen in vielen Sprachen ausgewertet.

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