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Biology, ecology and significance of longhorn beetles (Coleoptera: Cerambycidae)

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Abstract
Family Cerambycidae is one of the economically most important wood boring insect. It interferes and causes damages to forests, forest products, shade trees, fruit and nut trees, vegetable and field crops, seeds, orchids, and flowers. The long antennae, absence of a beak, and pseudo tetramerous tarsal segments serve to separate most adults of this very large family from other beetles. The grubs of most species develop for about one year or more in the tree trunk either as sap wood or heart wood feeder. Larvae of some species develop in highly decomposed wood, while others develop in herbaceous plants or roots. The infested trees may be killed and can have a major economic impact. Adults are relatively short lived, may feed on pollen and nectar of flowers, fungal spores or are attracted to sap flows on trees. The eggs are usually deposited under bark or in cracks in the wood with the help of the ovipositor. The larva is a stout, elongate, segmented, practically legless grub when full-grown, and is usually white or yellowish white or pale orange in colour. Larvae have strongly sclerotized mandibles capable of tunnelling the heartwood timber. Pupa usually lies quite naked in the pupal chamber at the tail of the larval tunnel. The microclimate of tree trunks, canopy and branches is a very important factor for this pest for normal growth and development.

Keywords: Longhorn beetles, Biology, Ecology, Pest

1. Introduction
Cerambycids are commonly known as longhorned beetles, longicorns, capricorns, round-headed borers, timber beetles, goat beetles (bock-käfern), or sawyer beetles, with body length alone varying from ± 2.5 mm (*Cyrtinus* sp.) to slightly over 17 cm (*Titanus giganteus)* and variety of shapes, coloration and ornamentation [1, 2, 3]. The recorded length (Kariyanna *et al.* 2016) of the Indian longhorn species is ranges from ± 3.5 mm (*Ropica* sp.) to ~12cm (*Acanthophorus serraticornis*).

The beetles are called longhorns because of their long antennae, especially in males. The long antennae and rather elongate bodies are used as general diagnostic characteristics of these beetles for identification [3]. However, longhorn beetles come in all sizes, shapes and colours, even commonly mimicking unpalatable beetles of other families, stinging ants or wasps and thus making a definition of the family rather difficult [3]. Longhorns are highly diverse, both taxonomically and ecologically, and are closely allied to their host plants. Thus, they may provide important data and evolutionary "clues" for ecological and zoogeographic studies [4]. Pioneering studies on longhorn beetles of the Indian subcontinent were made by [5-8]. Their contributions serve even today as an important baseline to take up holistic approach in documenting the longhorn beetles occurring in India. This review focuses on common biology, ecology and significance of longhorn beetles with special emphasis on their economic importance.

2. General biology of longhorn beetles
The adults of many species visit flowers where they feed on nectar and pollen, while others carry out feeding on bark in the crowns of trees. The mating can take place on the flowers or on the host plants [9] and copulation lasts from several seconds to several hours and repeated copulations with the same or a different partner are common although females may gradually become less receptive [10]. Beeson [8] explained that most cerambycid borers breeding in living plants without killing the plant or the portion tunnelled by the larva emerge in the rainy season and those that kill the plant may depart from this habit.

Cerambycids appear to be consistent in not showing any form of pre-copulatory courtship behavior; males typically approach females directly and attempt to mount and copulate [11]. However, Pheromones that act over long distances appear to be rather rare in the Cerambycidae, a circumstance that correlates well with antennal morphology. Schneider [12] revealed that the sensitivity to long-range pheromones in other insects is enhanced by increasing the surface area of the antennae, leading to the evolution of branched antennae that are lamellate, pectinate, serrate, *etc.* Such branched antennal morphologies are indeed evident in males of many prionine species [13], some of which apparently rely on pheromones for mate location. Other cerambycid species that use long-range pheromones (*Hylotrupes bajulus*, *Migdolus fryanus* and *Xylotrechus pyrrhoderus*) have antennae that are relatively short, like those of prionines, but differ little in structure between the sexes. An exception is that cerambycine *Strangalia bicolor*, which is believed to use pheromones [14]. However, these beetles are typically characterized by long antennae used mainly to detect pheromones allowing mating and the localization of the appropriate host plant for oviposition [15].

Blatchley [16] speculated that the elongate antennae of cerambycids provide balance when walking on slender twigs, as a pole does for a tightrope walker. But, Linsley [17] and Reitter [18] have not reported on the adaptive significance of elongate antennae in cerambycids, but sexual dimorphism in length has been taken as evidence that they play a role in mate location.

The life span of adults is usually measured in weeks or even days for many species, certain large Lamiinae are known to be active for several months under laboratory conditions when provided with food [8, 10]. But, Linsley [17] explained that, the knowledge on the natural longevity of emerged adult cerambycids is not completely known. However, the limited feeding of many species suggests that they are probably short lived.

The oviposition behaviour in longhorn beetles is very peculiar compared to another group of insects. According to Beeson [8], there are four methods of depositing the eggs by Cerambycid beetles: i) Oviposition on external surfaces of the bark in natural cracks or crevices into which eggs are thrust by ovipositors; eggs may be laid either singly or in groups (mostly all Cerambycinae); ii) Oviposition inside the bark in conical cavities or in slits gnawed by the mandibles down to cambium into which ovipositor is inserted and eggs are pushed between the sapwood and bark. Eggs are laid singly in this group (Eg. few Lamiinae like *Celosterna scabrator*, *Glenea* spp. *etc*); iii) Oviposition on converted wood devoid of bark, in natural or artificial fissures (Eg. *Stromatium barbatum*); and iv) Oviposition in soil (Eg. *Dorysthenes* (*Lophosternus*) *hugelii*). But, Linsley [17] concluded that least specialized groups morphologically have the simplest oviposition habits except for some Prioninae and Lepturinae which at the most embed the eggs in soft, decomposing wood. The most specialized habits are found in Lamiinae, which frequently utilize mandibles to prepare the oviposition site for their protection.

Morewood *et al.* [19] suggested that Coniferophagous species, such as *Monochamus scutellatus* (Say) (Cerambycidae), prefer large diameter hosts, or the largest diameter portion of a given host for oviposition, which would provide the most resources for the developing progeny. In contrast, many Lamiinae species (*Cerambycidae*) that attack hardwoods prefer smaller trees (> 20cm) in diameter and often much less. However, Stebbing [6] reported that the beetles invariably choose newly felled or green sickly standing trees in the forest for egg laying. As a general rule that, insect lays its eggs in crevices of the outer bark as near to the bast layer as possible or when occasions serve, at the edge of some wound in the bark. This is commonly the case with the poplar and willow longicorn beetle, *Aeolesthes sarta.*

Various investigators quoted different opinion regarding eggs of longhorn beetles. As per Švácha and Lawrence [10] reported that longhorn beetles are oviparous and their eggs are elongate, oval or fusiform to broadly elliptical and often have thin flexible chorion, and their shape can adapt to the tight spaces in which they are laid. Slipinski and Escalona [3] revealed that, the eggs of Cerambycidae are 1-7 mm long and single female usually lays 25-100 (up to 600) eggs during her life span. The eggs are hatch in one to three weeks [20] and the first instar larvae open the chorion using their mandibles or the egg bursters on the head, thorax and/or abdomen [21].

The larva is a stout, elongate, segmented, practically legless grub when full-grown, and is usually white or yellowish white or pale orange in colour; the segments taper slightly from the anterior end to downwards. And have powerful black biting jaws or mandibles, with which they are capable of tunnelling down into the hardest timber. The grubs have short, four-jointed antennae, and may have very short legs in some cases. The upper surface of the head and of the thoracic segments is covered with a hard, horny plate; the segments of the body have often tubercles on them, and the spiracles on the sides of the segments are well marked [6].

The larval instars of longhorn beetles feeding on the wood of healthy trees varied between 7 and 10 (Linsley, 1961). Larval development varies considerably but in most species usually takes one to three years, with the larvae of Prioninae taking the longest time on an average [13]. The development is very rapid in Lamiine species feeding inside stems of herbaceous plants and is usually completed within three months. In contrast, the species capable of developing in dry and processed timber have been known to emerge from furniture, timber or subflooring after many years. Early instar larvae usually feed under bark on cambium and phloem before entering the sapwood in the later stages, or to pupate. The pattern and the type of frass made by larvae in excavating the burrow are often characteristic for particular taxonomic or ecological groups of wood-boring Cerambycidae [13].

Most of the Cerambycidae larvae live in tunnels which are tightly packed behind with wood-dust but some species keep the tunnel clean by ejecting the frass through holes to the outside *viz*., *Aphrodisium, Apriona,* and *Celosterna* [10]. But, grubs of Lamiinae feeding in the wood always make straight tunnels, while those feeding on the bark make zigzag tunnels [8, 13, 17].

Pupa usually lies quite naked in the pupal chamber at the end of the larval tunnel. In India, the beetle *Plocaderns obesus*, Gahan, the larva constructs a calcareous cocoon resembling a pigeon's egg, in which it transforms to the beetle state [6]. According to Beeson [8] explication the pupal chambers of Indian Ceambycidae into various groups *viz.* (i) Pupal chamber without specially secreted lining; (ii) Pupal chamber with a specially secreted lining or operculum of calcium carbonate (secreted from Malpighian tubules) or other material; (iii) Pupal chamber in supporting tree in case of larvae boring lianas; (iv) Pupal chamber in soil. The pupal stage lasts between a week to a month and after eclosion teneral adult remains in the pupal cell for some time before it emerges through the exit hole [3].

The season in which emergence of the adults occurs is a characteristic of the species; four emergence-periods were are recognized *viz.,* summer, dry or pre-monsoon season, southwest monsoon season and post-monsoon season. Monsoon emergence is strongly influenced by the initial date of first showers, quantity and distribution of monsoon rainfall [7]. Once near the female, a male immediately makes an attempt to mount and copulate and 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 with many exceptions [17].

The eggs (one egg or a group of eggs) are usually deposited under bark or in cracks in the wood with the help of the ovipositor. Some species of the genera *Saperda* and *Monochamus* gnaw excavations into the wood and deposit a single egg in this hollow. During larval development, which mostly lasts 1–3 years, several larval stages (for example, up to 14 in laboratory rearing of *Anoplophora glabripennis*) are passed through, ending with pupation within characteristic pupal cells in the host tree [9]. The annual life cycle may be regarded as fundamental rhythm but it is characteristics of the species rather than of a climatic region or of a habitat [8]. But, the life-cycle in various Indian species ranges from two and half months to over 10 years. In temperate climates, the life-cycle is annual or longer; in the tropics, species with annual cycles are as characteristic of species with shorter cycles. In the majority of dead-wood borers, a brood normally consists of short-cycle and long-cycle larvae, so that development may be prolonged by multiples of the short period up to two or three years from oviposition [7].

3. Ecology of Longhorn beetles

Microclimate of tree trunks, canopy and branches is a very important factor for the forest insect pests. Similarly, Morewood *et al.* [19] suggested that the upper trunk and major branches, where the bark is relatively thin and smooth, are reportedly favored by *Anoplophora glabripennis* (Coleoptera: *Cerambycidae*). In accordance with Paulino-Neto *et al.* [22] *Oncidere humeralis* (*Cerambycidae*) females prefer *Miconia sellowiana* with more secondary branches, indicating that, apart from the trunk diameter, the number of secondary branches can also influence the plant choice for beetle attack.

Temperature plays an important role in the localization of insects that live in tree trunks. For example, the life cycle of the Cerambycid, *Monochamus scutellatus* is limited to one year in trunks exposed to sunlight and to three years in shaded trunks. Moreover, the subcortical and sapwood temperatures in trees and logs exposed to sunlight can be several degrees (5-30 ºC) greater than shaded portions [23, 24]. The warmer temperatures experienced on the sunny *versus* the shaded side of logs can cause a 1to 2 years difference in developmental time for phloem-feeding cerambycid beetles [23-25].

Dajoz [26] emphasized the importance of wind for the dispersal of certain insects and Maymoona [4] depicted that highest number of emergence holes of longhorn beetles were located on the south-side of the tree *Acacia mellifera* (63.6 %) and the highest number on *A. senegal* (83.3 %) was found on the west side. This could also be related to wind direction. As per Stebbing [6] longhorns are powerful fliers, and probably travel a considerable distance in search of suitable trees (storm), the incident proved that the beetles are sufficiently powerful to fly at night in heavy wind and rain.

Gillott [27] also found that rain probably exerts its influence on most insect populations indirectly, notably by affecting the availability and quality of food or the incidence of disease. But, Nair (28) argues that high rainfall amounts favor the development of the Cerambycid borer population *Hoplocerambyx spinicornis* on *Shorea robusta* (sal tree). Hanks *et al.* (29) claimed that, phloem-boring larvae may be especially vulnerable to moisture conditions because, they are embedded in the tissues of their host plant, and sensitivity to bark moisture could account for the association between drought stress and host susceptibility which is typical for many phloem-boring insects, especially Cerambycid beetles. Thatcher (30) revealed that, the greatest damage to *Megacyllene robiniae* (Forst.) (Coleoptera: Cerambycidae), a wood-boring beetle attacking living trees, coincides with drought conditions, as drought enables a larger number of larvae to survive. Speight and Wylie (31) also concluded that the mortality associated with attack of *Eucalyptus* plantations by *Phoracantha semipunctata* (Cerambycidae) was highest for trees planted in soils that had a high sand content.

4. Host plant relationships

The behaviour and reproductive strategies of adult cerambycids are shaped by host requirements of the larval stage (11). The larvae of most cerambycids bore into shoots, twigs, stems and roots of woody plants. A few small species develop in seeds while, others attack herbaceous plants (32). Some species of cerambycid beetles apparently do not use volatile pheromones, the sexes being brought together by their mutual attraction to host plants (33 & 34).

Hanks (11) differentiated four categories of cerambycids host selection, including healthy hosts (HH species), weakened hosts with recovery potential (WH species), severely stressed or moribund trees, including recently felled trees (SH species), and dead or decaying trees, including seasoned, structural wood (DH species). There are also distinct differences with respect to part of wood cerambycid larvae are likely to develop. Many HH and WH species feed relatively briefly in the subcortical area (inner bark, cambium and young sapwood) before spending the remainder of the developmental period in the sap and/or heartwood. SH species feed almost exclusively in the subcortical zone. However, Schabel (32) Claims they often occur in the outer sapwood but only invades it for pupation or if they should run out of subcortical tissues before reaching maturity.

5. Economic Importance of longhorn beetles

Cerambycidae is one of the economically most important groups of insects of the world. It interferes with and damages forests, forest products, shade trees, fruit and nut trees, vegetable and field crops, seeds, orchids, and flowers (17). Basically, the larvae of longhorn beetles are phytophagous and inflict damage by acting as borers of sapwood or heart wood by feeding on bark or phloem, and acting as root borers or sometimes gall formers. Larvae are known to develop in dead wood, live woody plant or herbaceous stems. Larvae are infrequently noticed feeding on cones or seed pods or entirely within the seeds. Few start their life in lianas/woody climbers and later make their transition to the wood of the supporting tree (8 & 10).

Longhorn beetles have received attention in the recent past because of their pest potential (29, 35 & 36). Remarkably, the larvae of *Microlamia pygmaea* Bates acts as leaf miner in dead leaves (37) and the larvae of *Pseudovadonia livida* (Fabricius) live on decomposing plant litter by feeding on hyphae of the underground fungi (38).

Adults are known to girdle twigs or branches for feeding.

Feeding on fermenting sap, fermenting fruit, pollen, nectar or fungal spores was also observed [8, 10]. Contrary to the phytophagous nature, the adults of *Elytroleptus* are carnivorous [39, 40]. Many species of longhorn beetles could damage both old as well as young trees [8, 4] and the deciding factors for their infestation are the nutrient content, moisture and temperature [41, 10].

Longhorn beetles of the genus, *Monochamus* are reported to transmit the pinewood nematode, *Bursaphelenchus xylophilus*. Pine wilt disease is reported to occur in East Asia, Europe, and North America [42, 43]. Primary vectors were reported to be different in the different continents; *Monochamus alterntus* in East Asia, *M. galloprovincialis* in Europe, and *M. calorinensis* in North America [44-47].

In the recent past, the Asian long-horned beetles are of quarantine concern in the USA and these beetles were reported across New York and Chicago, for the first time in 1996 causing extensive damage to hardwood trees. It was reportedly introduced from China through shipment material [48]. Further, this pest has invaded England [49] and Italy [50].

Longhorn beetles are among the most important insect pest's worldwide, degrading timber and injuring and killing trees in forests, plantations, and urban landscapes [1]. However, longhorn beetles are also fundamental to the decomposition of dead wood, incorporating plant parts to the ground and allowing the renewal of forests by opening spaces and consequent seed germination [51]. Similarly, some longhorn beetles may be valuable bio-indicators of forest health and useful for conservation as indicators of the destruction or fragmentation of their habitat [52-54]. However, some are beneficial insects through their role as insect pollinators on some plant species [55, 56].

Some species of long-horned beetles were used as biocontrol agents against weeds in different parts of the world. Cerambycidae, *Alcidion cereicola* Fisher was approved for release in Queensland, Australia for the control of *Eriocereus martinii* Lab [57]. The grubs of longhorn beetles are being used as food commodities and source of medicine in many tribal communities of North Eastern India. The grubs of *Batocera rufomaculata* and *Acalolepta cervina* are used as edible foods; whereas, the grubs of *Batocera rubra* (Synonym of *Batocera rufomaculata* DeG.), *Batocera titana* (Synonym of *Batocera numitor* Newman), *Celosterna scabrator* (Fabricius), *Neocerambyx paris* (Wied.) and *Xystrocera globosa* (Oliv.) have been used since ages in the folklore medicines in these areas [58, 59].

6. Damage on forest ecosystem / quarantine significance

Beeson and Bhatia (7) documented 350 cerambycid species, associated with 568 species of trees, shrubs, and woody climbers. The sal tree, *Shorea robusta* attracted the largest number of longicorns (37 species) and for the dry-wood borer, *Stromatium barbatum* F. 311 food-plants were listed.

There are three Asian species of lamiinae *viz.,* Asian longhorn beetle, *Anoplophora glabripennis*, citrus longhorn beetle, *A. chinensis* and pine sawyer beetle, *Monochamus alternatus* are serious pests of quarantine concern and their accidental introduction would be very damaging to the native and ornamental trees in Australia (3). Approximately 20 per cent of the European longhorn beetles are of forestry importance as technical pests for the timber industry [41].

The *Aeolesthes holosericea* (Fabr.) is recorded as a polyphagous pest infesting a wide variety of forest plants and trees [60]. Stebbing [6] recorded eight host plant species and Beeson (1941) documented nearly thirty-seven species of its host plants. Ambethgar [61] worked on the infestation and development of *Aeolesthes holosericea* on neem (*Azadirachta indica*) by inoculation of the grubs on its live stems in laboratory.

The larvae of *Hoplocerambyx spinicornis* (Newman) bore into the live bark and cause significant damage to the vascular system by feeding and tunneling the inner layer of bark, resulting in reduced nutrient uptake, premature leaf senescence, gradual shedding of leaves and death of the tree. The intensity of infestation and extent of damage varies widely across the regions. On an average, this borer kills about 2-5 per cent productive trees every year [62]. Nearly 6-35 per cent trees of neglected plantations were infested in Kerala, Tamil Nadu and Orissa [63-65]. In Andhra Pradesh (Guntur and Prakasam Districts), upto 40 per cent infestation was observed in the forest [66, 67]. Damage by *Hoplocerambyx spinicornis* in the forests is of a two-fold nature: (i) The grub feeds in and destroys the bast layer of the trees thus eventually killing the tree; (ii) the grub tunnels down into the heart-wood and thus spoils or ruins it for commercial purposes [6].

7. Conclusion

The intensive agriculture, severe deforestation coupled with global warming has resulted in many longhorn beetle species becoming serious pests of agriculture, plantations and forest crop causing unavoidable economic losses. Some longhorn species have permanently established outside their natural distribution range due to the significant increase of international marketing and exchanging materials, which has resulted in the severe setback on trade. Despite their immense economic and ecological importance, longhorn beetles belonging to the Cerambycoidea (including Cerambycidae, Vesperidae and Disteniidae) is one of the least studied groups of the order Coleoptera in India. As for the number of longhorn beetles, over 1200 species were known to occur in Indian region by 1940's. Another little over 300 species were added by next three decades. Now India having total of 1551 long horn beetles belongs to nine subfamilies and 445 genera. So, there is a great concern needed to study the pestiferous nature of these beetles with their detailed taxonomic information and host range.

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