FIBLD-ECOLOGICAL STUDIES ON MASS ERUPTION, SEASONAL LIFE-HISTORY, NOCTURNAL
FEEDING AND ACTIVITY RHYTHM, AND PROTECTIVE BEHAVIOUR AND COLORATION IN THE
SAL DEFOLIATOR, LYMANTRIA MATHURA
(LEPIDOPTERA: LYMANTRIIDAE),
IN SUB-HIMALAYAN FORESTS

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(7 Plates, 6 Text-figures, 3 Tables and an Appendix)

Introduction

Lymantria mathura Moore (Lepidoptera: Lymantriidae) is a moderate-sized moth (Pls. 1-3) which occurs all along the Indian Sub-Himalayas from western Uttar Pradesh to Assam, and also extends farther east to Southeast Asia. There is marked sexual dimorphism in size and colour. The male is smaller (wing expanse 33 35-40 mm. \$\times 75-95 mm), with the forewings brown and hindwings yellow. In females the forewings are white with dark markings, and the hindwings pink. In Indian forests this species is an important defoliator of 'sal' (Shorea robusta, a forest tree of great economic importance) and of a few other species of trees. In normal years it occurs in small numbers, but periodically its population erupts, and millions of caterpillars may be seen defoliating large stretches of forests. Although often referred to as a pest in literature on forest entomology (Stebbing, 1907, 1908; "India", 1931; Roonwal, 1953-57; S. M. Singh, 1954; Chaudhuri, 1962; Roonwal, Chatterjee and Thapa, 1962), its ecology and seasonal life-history are inadequately known.

The most serious eruption, that of 1953-54, in the Western Sub-Himalayas (the Doon Valley and some neighbouring forests of Uttar Pradesh) provided the opportunity for studying various aspects of its field-ecology. In the present account are presented field-ecological data on: the mass egg-laying (on 185 species of trees); the progress of the epidemic, and its decline in 1954 (mainly as a result of mass mortality caused by a polyhedral virus disease); the seasonal life-history; a rhythm of nocturnal feeding and activity in caterpillars; colour forms; and protective behaviour and coloration in caterpillars.

MASS ERUPTION IN THE SUB-HIMALAYAS

1. The eruption of 1953-54

In the middle of September 1953, evidence started coming in of a mass increase of moth population in the New Forest area near Dehra Dun (the Western Sub-Himalayas, c. 610 m altitude, Uttar Pradesh), and by the end of the month the whole forest was full of these moths, laying eggs in masses (Pl. 3) on trunks of hundreds of trees (Roonwal, 1953, preliminary note). These eggs hatched next spring and produced millions of caterpillars which were seen on the trunks of trees in New Forest as well as the neighbouring forests in the Dehra Dun and Saharan-pur Forest Divisions, covering an area of over 1,000 km². In April the caterpillars and pupae were struck by a polyhedral (or "liquefying", virus disease which caused extremely high mortality, up to almost 99 per cent, and nearly wiped out the population. Very few moths emerged, and the eruption was over.

The 1953-54 eruption is the largest on record. It was not confined to the Western Sub-Himalayas, but extended as far east as West Bengal, some 1,200 km away, in the 'terai' and 'bhabar' forests of the Nimati Old Plantation of *Shorea robusta* in the Buxa Forest Division, as reported by Chaudhuri (1962) who found, in 1954, "millions and millions of larvae" defoliating sal.

2. Mass egg-laying, and subsequent restriction of food-plants

In normal years, Lymantria mathura lays eggs on, and defoliates, hardly half a dozen species (Beeson, 1941, 1961), viz., Shorea robusta (the principal food-plant), Syzigium cumini (syn. Eugenia jambolana), Quercus incana, Q. serrata, Terminalia arjuna and T myriocarpa. During an epidemic eggs are laid on a much larger number of tree species (185 in the 1953 epidemic, vide Appendix), and the numerous white egg-mass patches form a conspicuous sight on the dark tree trunks in the forest. On most of these species the larvae die early, and ultimate defoliation occurs on barely 22 species of trees.

In the New Forest Survey over an area of about 10 km², egg-masses were recorded on 405 trees, the number varying from 1 to 223 egg-masses per tree. The broad preference for each species was determined on the basis of the number of egg-masses on a tree, but the prevalance of attack should also be kept in view. Thus, a species with fewer egg-masses but universal attack may perhaps be regarded as more preferred than one with more numerous egg-masses but with many trees free from attack. For a rough estimation, preferences were grouped into three classes as based on the average number of egg-masses per tree as follows (also vide Appendix):

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Preference small (S) : Below 10 egg-masses per tree moderate (M): 10-40 ,, ,, ,, ,, ,, ,, ,,
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On this basis, the moth showed for egg-laying a medium degree of preference for 23 species ("M" in Appendix), and great preference ("G") for the following seven species:

Dipterocarpaceae: Shorea robusta Lauraceae: Cinnamomum camphora

Meliaceae: Cedrella toona

Myrtaceae: Syzygium cumini (syn. Eugenia jambolana)

Rutaceae: Aegle marmelos

Urticaceae: Ficus racemosa and F. religiosa

These eggs hatched next summer. An extensive survey of the New Forest area carried out in the first week of April 1954 (when larvae were already large, c. 20-75 mm long) showed the presence of larvae on only 22 species of trees amongst which they were especially abundant on the following six heavily defoliated species: Acrocarpus fraxinifolius, Mangifera indica, Quercus incana, Shorea robusta, Syzygium cumini, and Terminalia myriocarpa. The larvae survived ion ionly a fraction of the 185 species on which they oviposited; on the others they died in the early stages. That there are definite host preferences is further suggested by the following observation in New Forest. In one place there are two straight rows, 6 m apart, of 18-24 m high trees, each about 3 m apart, of two species, viz., Acrocarpus fraxinifolius and an undertermined species, each alternating with the other. Larvae were present only on A. fraxinifolius, leaving the other species entirely untouched. Again, in April 1954, in a mixed forest not far from Dehra Dun (Mohand Range, Saharanpur Forest Division), Shorea robusta and Syzygium cumini were badly defoliated but the neighbouring trees of Terminalia tomentosa were untouched. Although the latter species is known to be one of the food-plants of L. mathura, it was apparently avoided in the presence of the preferred ones. So far, the following 32 species have been recorded as being defoliated by Lymantria mathura (the list includes new as well as old records):—

Anacardiaceae: Mangifera indica.

Apocynaceae: Alstonia scholaris.

Celastraceae: Eleodendron glaucum.

Combretaceae: Anogeissus lalifolia, Terminalia arjuna, T. belerica,

T. myrciocarpa, T. pyrifolia and T. tomentosa.

Cupuliferae: Quercus incana and Q. serrata.

Dipterocarpaceae: Shorea robusta. Euphorbiaceae: Mallotus phillipinensis.

Fagacoae: Castanea sativa.

Leguminosae:

Caesalpineae: Acrocarpus fraxinifolius.

Papilionaceae: Butea monosperma and Pongamia glabra.

Lythraceae: Duabanga sonneratioides.

Meliaceae: Ammora rohituka, Cedrela toona and Melia azedarach.

Myrtaceae: Syzygium cumini (syn. Eugenia jambolana).

Rosaceae: Prunus puddum. (Burma)

Rubiaceae: Adina cordifolia and Anthocephalus cadamba.

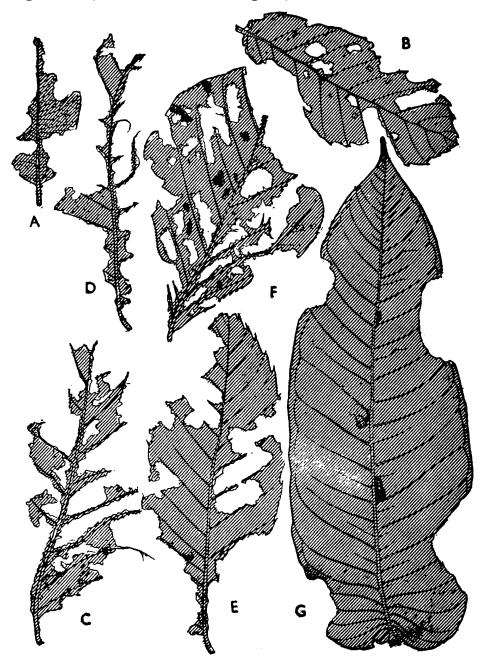
Sapindaceae : Litchi chinensis. Sterculiaceae : Sterculia alata. Tiliaceae : Grewia sapinda.

Urticaceae: Artocarpus lakoocha, Ficus bengalensis and Morus alba.

Interestingly, this list excludes four of the seven species on which heavy egg-laying took place in the 1953 eruption, viz., Cinnamomum camphora, Aegle marmelos, Ficus racemosa and F. religiosa.

Nature of feeding

The larvae eat mostly the green parts of the leaves, the thicker veins are generally avoided (Text-fig. 1).



Text-fig. 1.—Pattern of defoliation by Lymantria mathura on leaves of various food-trees. Mostly the green parts are eaten. (Not to scale.) (A) Syzygium cumini. (B) Quercus incana. (C) Shorea robusta. (D) Castania sativa. (E) Butea monosperma.

(F) Terminalia myriocarpa. (G) Duabanga sonneratioides.

SEASONAL LIFE-HISTORY

1. Number of annual generations (Table 1 and Text-fig. 2)

Little is known of the life-history of Lymantria mathura in India-Beeson (1941) mentions two broads in summer (with larvae in April and again in the rains, June-August), and a second generation in September-October. (In Japan, Nishigaya, 1918, studied the life-history on apple, but this was evidently of the subspecies L. m. aurora Butler.)

STAGES	J	F	Μ	Α	M	J			Α	S	0	N	О
		FIRST OR SUMMER GENERATION											
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LARVAE							_			-	,		ı
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Text-fig 2.—Lymantria mathura. Chart to show life-history in the Western Sub-Himalayas (Dehra Dun forests, altitude 610 m).

The present study shows that in the Western Sub-Himalayas (Dehra Dun forests, altitude 610 m) Lymantria mathura has two annual generations (Table 1 and Text-fig. 2)—a short first or summer generation (April to October), and a long second or overwintering generation (September to June) with a diapause in the egg-stage.

Eggs are laid in masses on tree trunks. In both generations the larva undergoes five moults and has six instars. Larvae are gregarious. Pupation also occurs in groups of 40 or 50, usually in dark, protected places such as debris at the base of trees or behind signboards hanging from tree trunks, but sometimes also in exposed places.

Males are seen much less frequently than females and they die at least a week before the latter. Females are sluggish; after egg-laying, they can be seen sitting on tree trunks in groups of six or more near. egg-masses. If disturbed, they slowly move away a little but do not fly

Table 1.—Seasonal life-history of Lymantria mathura in Western Sub-Himalayas from insectary rearings at Dehra Dun, supplemented by field observations. (For the presence of different developmental stages in nature, see Text-fig. 2.)

Egg-laying an		Dur		Eclosion of	Death of					
Egg-laying by moths of previous generation	Incubation period	I stage	II stage	III stage	IV stage	V stage	VI stage	Pupa	moths	moths
	FIRST OR	SUMMER	GENERA	ATION (A	APRIL TO	ОСТОВ	ER)			
Mid-April to mid-June	About 3-4 weeks (?)	34	3—5	4	3	6	?	712	End of July to 3rd week October	All dead by end of October
	SECOND O	R OVERV	VINTERIN	G GENER	ATION (SEPTEME	ER TO J	JNE)		
Early Septemb e r to end October	160—178	9—28	3—17	2—11	2-8	5—1	1 ?	10—11	Mid- April to mid-Juno	All dead by end of June

(a) The first or summer generation (April to October)

Moths of the overwintering generation lay eggs from mid-April to mid-June; these eggs hatch in three to four weeks. There are six larval instars. Larvae are met with in the field from early June to end-September, and pupae from the third week of July to the third week of October. The durations of instars, in the Dehra Dun insectary, were as follows: Instar I, 3-4 days; II, 3-5; III, 4; IV, 3; V, 6; VI, (?). The pupal stage lasted from 7 to 12 days. Moths emerged from the end of July to the third week of October, and laid eggs from early August to the end of October; all were dead by the end of October.

(b) The second or overwintering generation (September to June)

Eggs laid in autumn (early September to mid-October) at first developed quickly, and in about six weeks the larva was fully formed, complete with its long hairs, and even the sclerites of the head and body were fully and deeply pigmented. The egg now had a dark appearance, with the dark sclerites showing through the translucent egg-wall. In this stage it entered a diapause of four to five months and hatched next spring (February to early April). The minimum period for this overwintering generation was about seven months; approximate individual periods (in days) were: egg 160, larval 27, pupal 10, and adult about 15 days. The various stages of the second generation continue to be met with in the field for nearly 10 months (Text-fig. 2) from early September to the end of June next year. Details are discussed below.

Hatching occured next year (after a long overwintering diapause of the fully formed embryo in the egg) from the third week of February to the first week of April (18 February to 3 April). The incubation period was 160-178 days (166-168, in 45% of the cases). Larvae were me with in the field from the third week of February to about the end of May. The duration, in days, of the various instars was as follows (it shortened considerably as the weather warmed up):—

Instar I: 9-28 days. Hatchings of late February had longer (12-28 days, mostly 22), and those of March shorter durations (9-13 days, mostly 11).

Instar II : 3-17 (mostly 4-7).
Instar III : 2-11 (mostly 5-7).
Instar IV : 2-8 (mostly 5-7).
Instar V : 5-11 (mostly 6-7).

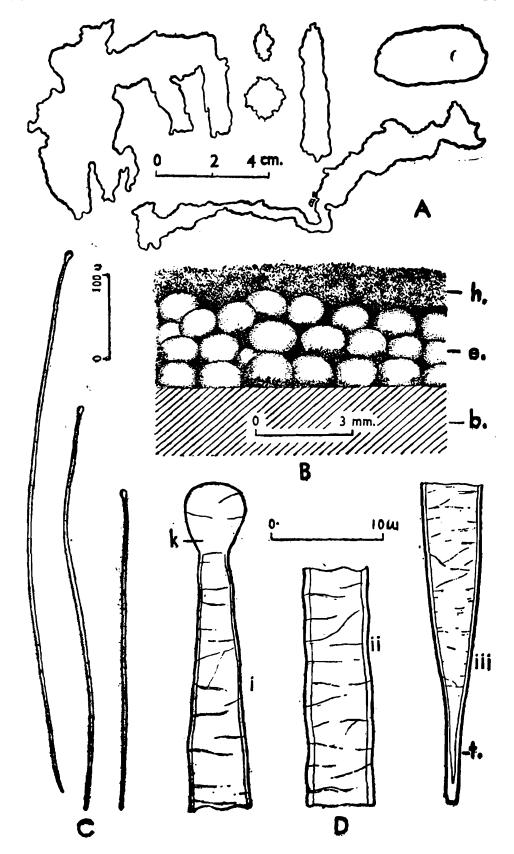
Instar VI: Not known (larvae died in large numbers due to a polyhedral disease). Mature larvae were common in the field throughout April.

The pupal stage lasted 10-11 days. Pupae were found from early April to mid-June, or later. Moths emerged from the second week of April to mid-June, or later. Eggs were laid from mid-April to the last week of June. All moths were dead by the end of June.

2. Egg-laying and hatching

Egg-laying

Eggs are laid on the bark of trees in flat, hair-covered egg-masses



Text-fig. 3.—Lymantria mathura. Egg-masses and covering hairs. (Adapted from Roonwal, 1954.) (A) Surface view of six egg-masses, to show different shapes and sizes. (B) Part of egg-mass, in transverse section. (C) Three hairs from hair covering of egg-mass. (D) Same, one hair, enlarged (i- iii, knobbed end, middle part, and truncated end respectively).

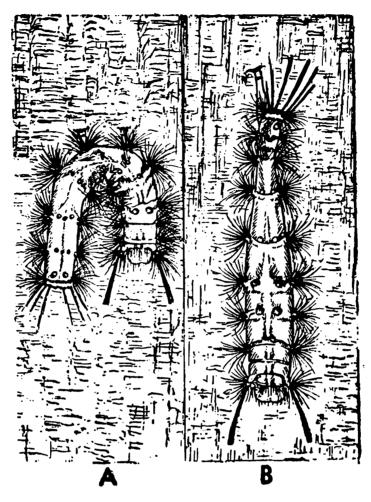
(Pls. 3 and 4; and Text-fig. 3). In normal years they are laid on a limited number of species, barely half a dozen, which are the common foodplants of larvae. In epidemic years, however, they may be laid on a large number of species (185 were recorded here in the 1953 epidemic) and, exceptionally, elsewhere such as on the upper surfaces of dried flowers and fruits, and even on brick walls and wire-netting. The female prefers a rough surface for laying, as shown by the following observations: In eucalyptus trees the bark is often either wholely or partly shed, exposing the smooth silver-grey trunk. Eggs were laid only on the rough, bark-covered portions. They were entirely absent on the smooth, barkless parts; trees wholely devoid of bark had no egg-masses at all. Eggs-masses are laid from ground-level up to about 18 m (60 ft.) of the trunk, but are most dense between the levels of 0.5 to 5 m. They are flat, of an ovoid-elongate or other shape, with irregular edges, and vary in extent from about 0.5×1 cm to 6×15 cm. From a distance the egg-masses are visible as characteristic white, fluffy patches against the dark-coloured bark (Pls. 3 and 4; and Text-fig. 3A). Each egg-mass contains about 50 to 1,200 or more eggs which are laid 2 to 4 layers deep directly on the bark (Text-fig. 3B). An egg-mass is covered over with a nearly one-millimetre, white thick felt-like covering composed of long, white, silken hairs. (According to Wileman, 1918, these hairs are shed by the female from the anal tuft. A similar habit was noted by Janjua, 1950, in another lymantriid, Euproctis signata, in Baluchistan.) The hairs are about 800-1200 μ long and 3.1-6.2 μ in diameter; one end is knob-like, the other pointed (Text-figs. 3C, D); a few such hairs are also mixed with the eggs. (For more details of hair structure, see Roonwal, 1954.) Freshly laid eggs (Pl. 4, Fig. 4) are rounded, have a flat base, the maximum and minimum diameters varying from 1 13-1 19.mm. and 0.86-0.92 mm respectively.

After egg-laying the females are very sluggish and continue to rest for days near the egg-masses; having no proboscis, they take no food. If disturbed, they move away a little but do not fly; ultimately they die and drop to the ground.

Egg-mass after hatching

After the majority of eggs have hatched, an egg-mass presents a changed appearance. Firstly, the hair-covering which has hitherto (for several months in the case of the overwintering eggs) remained pure white, now becomes dull-coloured—a dirty cream and, in a few cases, with irregular patches of pale buff. Secondly, the hair covering is pierced by numerous rounded holes of varying diameters (c. 0.5-3 mm) through which the newly hatched larvae have escaped (Pl. 4, Figs. 7 and 8.) Beneath the thin, hole-pierced, hairy covering, there is

a flat, hollow space containing the remanants of egg-shells and a few remaining eggs which have not yet hatched.



Text-fig. 4.—Lymantria mathura. Two fully-grown female caterpillars, dying from polyhedral (or "liquefying") disease, and hanging in characteristic positions by means of one or two prolegs. (A day later they were dead.) (A) Hanging by means of two of the middle prolegs. (B) Same, hanging by a single, hindmost proleg. (New Forest, Dehra Dun, mass eruption, April 1954. The disease killed millions of caterpillars and pupae and controlled the epidemic.)

For two to three weeks the young larvae remain in a dense group on the hair-covering, crawling slowly over it and sometimes underneath the covering. How, and whether, they feed during this period is not known. In the laboratory they were given fresh leaves and nibbled at them, but several hardly ate, and died; in nature there is considerable mortality in this early stage.

3. The larval instars

(Pl. 1, Figs. 5 and 6; Pl. 4, Figs. 3-6; Pls. 6 and 7)

The size and colour characteristics of the six larval stages are given below briefly; the various colour forms and protective coloration of the older larvae are discussed later.

Stage I. Length 3 mm; head-width 0.5 mm. Generally black dorsally; meso- and metathorax and segment 5 of abdomen brown; legs black; prolegs pale brown with a black patch externally.

Stage II. Length 5 mm; head-width 0.7 mm. Generally black dorsally; meso- and metathorax greyish; last abdominal segment pale brown with blackish tinge; rest as in Stage I.

Stage III. Length 13 mm; head-width 1 5 mm. Head brown; body black above, paler below; thoracic terga with yellow-brown spots; legs black, prolegs brown with a black external patch.

Stage IV. Length 20 mm; head-width 2.5 mm. Head above either black (brown distally) or pale green with black dots; sides brown; body black with white warts; meso- and metathorax with brown stripes anteriorly; legs and prolegs as in Stage III.

Stage V Length 30-40 mm; head-width 3.5 mm. Head above brown to grey, speckled with black; body black with many minute white spots; pro- and mesothorax with a transverse brown streak at the distal edge; ninth abdominal segment with a pair of prominent dorsal white spots; legs and prolegs reddish brown, the latter with a large black patch externally.

Stage VI. Length 60-85 mm; head-width 5-6 mm. With sexual dimorphism, females being longer (35 60-65 mm, \$\pi_i 70-85 mm)\$. Colour pattern similar to Stage V, but in ground-pattern three types recognizable, viz., grey-white, blackish-brown and intermediate (vide infra). Older larvae well "camouflaged" against tree trunks. (A morphological description has been given by Gardner, 1938.)

4. The pupa

(Pl. 1, Figs. 7 and 8)

The pupa is of the "obtect adecticus type", and the appendages are firmly soldered to the body. It is buff to dark brown, about 20-36 mm long, and shows sexual dimorphism; the female pupa is paler, larger and heavier than the male, as follows: Female: Buff to pale brown. Length (including hair tufts) 30-36 mm; maximum width 10-14 mm. Weight 0.88 gm (average of 18 pupae). Male: Very dark chocolate brown. Length (including hair tufts) 15-25 mm; maximum width 6-8 mm. Weight 0.14 gm (average of 53 pupae).

426 pupae of the second (overwintering) generation obtained in the field in April showed a preponderance of males (33 58%, 99 42%).

PREDATORS, PARASITES AND DISEASES

1. Predators

Caterpillars are cryptically coloured. They merge perfectly with the background (bark of tree trunks) and are almost impossible to detect when at rest (vide infra). During the eruption years, 1953-54, when caterpillars were present in millions in the Doon Valley forests, I saw only one case when a bird predator (the Common Myna, Acridotheres tristis (Linnaeus)) caught and ate a large caterpillar.

2. Parasites

Owing to heavy death by a polyhedral disease (vide infra), barely 3 %, or less, of the larvae survived in the breeding cages. The surviving larvae were rather heavily parasitised by some Hymenoptera (undetermined chalcids and a braconid, Apanteles sp.) and Diptera (undetermined tachinids)). The pupae were moderately parasitised by tachinids.

3. Polyhedral disease

In the first week of April 1954, the larger caterpillars (4th to 6th instars) started dying by a "liquefying" or polyhedral virus disease which spread rapidly and drastically reduced the larval population-Death from this disease progressed rapidly, thus: April 2nd, 2 % of the population was affected; 9th, 8%; 12th, 52%; 14th, 99%. By the middle of April nearly the entire larval population was wiped out. The disease was also prevalent among the pupae, but the incidence of deaths was lower (April 6th, 13%, 22nd, 28%). The disease occurred not only in the field but also in the insectary, having apparently been introduced from material brought in from the field. The symptoms and progress of the disease are as follows: Caterpillars become sluggish and stop feeding (as when they are about to pupate). Within 24 hours the body becomes limp and the caterpillars die. In these few hours the internal tissues decompose quickly and liquefy, and nothing is left except the outer cuticle. If the skin is pricked there oozes out a pale greenish white liquid which quickly turns dark brown or blackish purple on exposure to air. Dead caterpillars are seen hanging from tree trunks in a characteristic posture, by means of the crochets of either one or two prolegs (Pl. 5, Fig. 4; and Text-fig. 4). Pupae decompose in the same way as caterpillars.

The organism responsible for the disease was identified by the Virus Research Unit of the Molteno Institute, Cambridge, England, as a "rod-shaped virus infecting the nucleus of cells of the insect." The disease effectively controlled the moth epidemic, and there was no sign of any abnormal population in the immediately succeeding years.

The source of the infection is not known and may be latent, the infection becoming virulent and conspicuous in periods of population eruption. Evidence of latent infection in larvae has been adduced in other Lepidoptera also (Kovacevic, 1954).

NOCTURNAL FEEDING AND ACTIVITY RHYTHM IN CATERPILLARS

Freshly hatched caterpillars remain on the surface of the hairy covering of egg-masses (Pl. 4, Figs. 5 and 6) for about two weeks and apparently do not eat. After some time they move out slowly in search of tender leaves for food. Since in the case of tall trees, on whose trunks the eggs are often laid, the tiny larvae have to climb a great distance to reach the leafy crown, many die in the course of this journey. Even in laboratory eages there is considerably mortality.

1. The nocturnal feeding and "migration"

In the younger stages there is no fixed feeding time, and larval movements on tree trunks are irregular. By the fourth stage feeding occurs almost entirely at night, for which purpose the caterpillars crawl up the tree trunks. The daily nocturnal "migration" up and down the tree are regularly timed. They were closely observed in April when the caterpillars were well developed and mostly in the fifth and sixth stages.

Apart from short-term observations on many nights, sustained all-night observations on timings of the daily night movement were made on four successive nights (April 2, 3, 4, and 5) in New Forest, near Dehra Dun, on trees of Acrocarpus fraxinifolius Wight (Leguminosae: Caesalpineae). This is a tall tree with a straight bole, and grows to a height of about 21-24 m (c. 70-80 feet) or more. It has a girth (at breast height of 1.3-1 5 m, a crown-height of 3-6 m, and a spread of the same dimensions. The bark is thin, brownish grey and rather smooth. Tree heights were measured in the day along with those of smaller trees nearby to serve as markers during the night. A pair of field binoculars was used to observe the caterpillars lying high up. Night observations required the aid of a powerful electric torch. The following is a brief account of the principal findings.

Throughout the day the caterpillars remain at rest, closely packed in large irregular patches and strips on tree trunks (Pl. 5, Figs. 1-3), extending high up even to the main branches but totally absent on the leafy crown. A considerable proportion of the population is concentrated on the basal 1 5 metres of the trunk, where the average density is 629 caterpillars per square metre (Table 2). A large tree on the basal

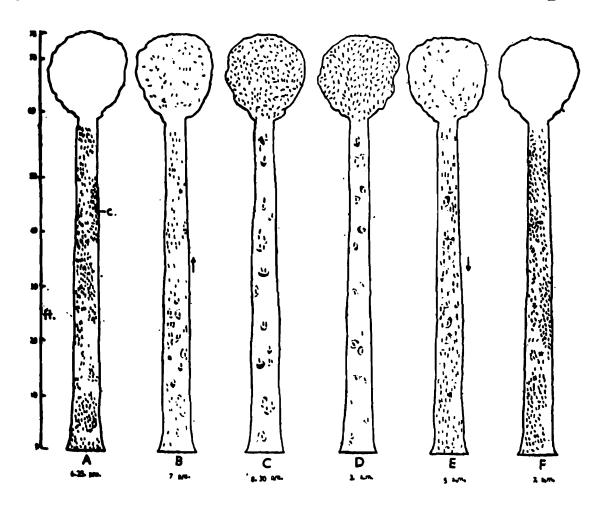
Table 2.—Lymantria mathura. Population of fully-grown caterpillars on lower portion (base to 1.5 m) of trunks of Acrocarpus fraxinifolius before and after the evening migration upward (New Forest. Dehra Dun, 3rd April 1954).

Tree No.	Girth (in m)		Surface area of trunk from		and density of es at 5 p.m.	Number e	es at 9 p.m.	Number etc. of caterpillars at 1 a.m.	
	At base	At 1.5 m	base to 1.5 m (in sq. m.)	No. present	Density per sq. m.	No. present	% in terms of numbers present at 5 p. m. (col. 5)	No. present	% in terms of numbers present at 5 p.m. (col. 5)
1	2.1	1.5	2.4	1,368	570	287	21.1 %	267	19.5 %
2	1.9	1.2	1.9	1,140	600	206	18.1 %	201	17.6 %
3	2.1	1.5	2.3	1,173	510	287	24.5 %	283	24.2 %
4	1.9	1.3	2.0	1,671	836	264	15.8 %	247	14.8 %
		Average	2.15	1,338	629	261.5	19.9 %	249.5	19 %

1.5 m harbours, on an average, of about 1,338 caterpillars, and an estimated seven or eight thousand on the entire trunk.

During the day time resting period, caterpillars assume a variety of positions (Pl. 5, Fig. 2): some with the head pointing downward, others upward or to the side. The majority of them lie straight but a few may assume curved positions; all are closely adpressed against the bark. Most of them remain still, but an odd individual or two may be seen crawling sluggishly either upwards or downwards. When a caterpillar is touched with a stick, it either remains motionless or crawls a few centimeters away and then comes to a halt.

As dusk approaches some movement of the larvae is noticeable, and there is remarkable regularity in the timing of subsequent activity (Text-fig. 5). At about 6.25 p.m. all is still, but by 6.40 a few of the smaller caterpillars (fully-grown males and younger females) begin o show some activity: they twist and turn their bodies for a minute or two in a peculiar manner (described below), and then start crawling up the tree. By 7 p.m. a mass movement has developed and almost



Text-fig. 5.—Lymantria mathura. Rhythm of daily nocturnal "migration" of caterpillars to tree-crowns for feeding on leaves. Diagrammatic. The upward migration begins about 6.40 p. m., and is completed in an hour or so; the downward migration begins about 4.00-4.30 a.m. (a little before dawn), and is completed by about 7 a.m.

half the population is actively and purposefully crawling up the trunk. By 8.30 or 9 p.m. the bulk of the population has gone up and is vigorously feeding on the leaves high up, as indicated by the incessant dropping of excreta. On some trees the trunk is completely, or almost completely, bare by now, all the caterpillars having crawled up. On others, however, a small proportion of the population (about one-fifth, vide Table 2), remains unaffected by the mass movement and these individuals remain on the trunk throughout the night. Possibly, these apparently exceptional individuals either go up irregularly to feed, or have stopped feeding prior to pupation.

Feeding goes on vigorously throughout the night. At one a.m. in the morning the trunk is still almost deserted. From amongst those which had remained behind, a few caterpillars have ascended, but the number remaining is essentially unchanged. A few caterpillars slowly come down the trunk. Another odd caterpillar or two, may start to crawl upward. Overhead, the caterpillars are feeding vigorously and incessantly dropping excreta pellets. At 3 a.m. the scene is unchanged.

Shortly before dawn, the downward march begins. At first, about 4 a.m., the caterpillars come down the trunk in twos and threes, but quite fast; and shortly after, large numbers descend. By 5 a.m. an army of caterpillars is descending some caterpillars have already come to a halt at various points on the trunk; others have reached the very bottom and are stationary; and the remainder are actively marching down. At 6 a.m. the downward march continues actively, but many, have already settled down on the trunk. By 7 a.m., practically the entire population is back on the trunk and is at rest and only an odd caterpillar or two is travelling downward. They will remain at rest throughout the day until the cycle of activity commences again at dusk.

The practical importance of this daily rhythm is that dusting of insecticides or banding of trees by means of sticky bands (to prevent caterpillars from going up the tree) (vide Roonwal, et al., 1962) must be carried out during the day between the hours of eight in the morning (i.e., after they come down from the tree-tops and have settled down to rest) and six in the evening (i.e., before they start moving up).

In addition to these daily rhythmic movements up and down the same tree, which may be circadian, the caterpillars sometimes migrate from one tree to another in smaller numbers and for no apparent reason. In younger stages they sometimes hang by a silken thread from branches of trees and are blown with the wind to neighbouring trees, and thus they are spread from tree to tree.

Discussion: A somewhat similar but diurnal rhythm was noticed

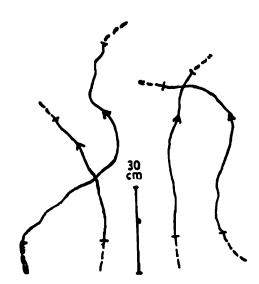
D. Singh (1973) in another lymantriid, Euproctis lunata Walker, in India. The last instar larva is active in the morning and early afternoon, between 6.30 a.m. and about 3 p.m., the peak of activity lying between 8 s.m. and noon. During the inactive period, the larva simply rests on the host leaves (castor plant).

2. Peculiar body-movements of caterpillars

As mentioned above, immediately before starting on the evening march up the tree trunk, the caterpillars, which have been sitting still all day, undertake, for a minute or so, a peculiar and characteristic turning and twisting of the body as if they were toning up their muscles after the day-long stupor (reminding one of the yawning and stretching of a person on waking up after a long sleep). During these movements the middle portion of the body remains attached to the tree surface by means of either two or three of the middle prolegs of the abdominal segments 4, 5 and 6 (there are five pairs of prolegs: a pair each on segments 3, 4, 5, 6 and 10), while the anterior and posterior portions of the entire body are repeatedly bent toward each other and partly moved from side to side. No sooner is this process over, than the caterpillar starts on the upward march. Occasionally, after covering a little distance, it stops and repeats these movements.

3. Speed and direction of movement

The caterpillars crawl purposefully in an irregular, sinuous band (Text-fig. 6) whose general direction is upwards. At a stretch, about 40-90 cm are covered; then a halt of a few seconds to a minute or so is called, after which the march begins again. The average speed of



fient-fig.—Lymantria methura. Portions of paths of progression of four full-grown caterpillars on a trunk during the evening ascent.

progression is 65.5 cm per minute, as judged from observations on four separate individuals (Table 3). At this rate, and assuming that a

Table 3.—Lymantria mathura. Speed of ascent of fully-grown caterpillars on trunk of Acrocarpus fraxinifolius. (New Forest, Dehra Dun, 5th April 1954.)

S1.	Approximate	Distance travelled						
No.	length of	(including curves)						
	caterpillar	at a stretch in 1						
	(cm)	minute (cm)						
1	5	67						
2	4	60						
3	5	45						
4	6	90						

Average speed: 65.5 cm per minute

caterpillar travels straight up and not zig-zag, it will take a minimum of about 28 minutes to reach the top of a high tree, with a 18 m (or c. 60-foot) high bole, where it is to feed. If half as much time is added for the zig-zags, and another 20 minutes for halts after each stretch of journey, a fully-grown caterpillar, travelling from the base of the tree, would take at least an hour to reach the feeding area. For smaller caterpillars, the time taken must be considerably longer. On the downward journey at down, the caterpillars move appreciably faster, as judged visually.

COLOUR FORMS AND PROTECTIVE BEHAVIOUR AND COLORATION IN CATERPILLARS

1. Colour forms

Three main colour forms (Pls. 6 and 7) are found in mature caterpillars, the following proportions being noticed in 1,613 caterpillars examined: grey-white 66 %, intermediate 11 %, and blackish brown 23 %. The details of colour are described below briefly.

Form I (Grey-white): Ground colour dirty white tinged with grey. Dorsal: Head white with numerous black or brown spots; frons with a longitudinal median black streak; rest of body grey-white, with numerous fine dots forming paired patches. A transverse yellow-brown streak present between pro- and mesothorax, and another in middle of metathorax: abdominal warts blackish; paired lateral papules on abdomen white, with tufts of long white and brown hairs. Long pencil-

like plumes of hairs on head and on end of abdomen black. Ventral: Brownish pink; legs and prolegs brown, the latter with a black patch externally.

Form II (Intermediate): Dorsal: Ground colour pale brown, with a median white patch on abdominal terga 4 and 5. Ventral: As in Form I.

Form III (Blakish brown): Dorsal: Ground-colour dark brown to almost black; numerous black spots visible in brown larvae but merged with ground-colour in darker ones; several small white dots present on abdominal terga 4 to the last, and large white patches on terga 4-6. Ventral: Ashy, suffused with a little pink in the median parts; rest as in Form I.

In the masses of caterpillars on tree trunks the various colour types are mixed on individual trees; this fact has a protective value by making detection by enemies difficult.

2. Protective behaviour and coloration

Although the masses of caterpillars are fully exposed during the day, they are completely free from the attention of birds which would normally make short work of them were they to detect their presence. Except an odd bird which caught and ate a caterpillar, no bird or any other vertebrate was ever seen predating on them.

The caterpillars show protective behaviour and coloration. They remain at rest on tree trunks throughout the day and seldom stir. At dusk they start crawling up the trees to feed on crown leaves, and descend at dawn. As mentioned above, the general colour of the mixed colour varieties forms a pattern which resembles the bark of trees very closely; this is especially so on the favoured host trees, Shorea robusta and Acrocarpus fraxinifolius. The resemblance to the background is so close to the human eye that although caterpillars were present in thousands in large patches or tree trunks, people passing within two metres of them often faild to notice them. Even children, who are usually very observant, missed them although every day they passed within two metres of the infested trees. The protective resemblance is especially perfect when the overall pattern, composed of different individual colour-forms, closely resembles the bark.

ACKNOWLEDGEMENTS

I am indebted to several staff members, especially Mr. Balwant Singh, of the Entomology Branch, Forest Research Institute, Dehra Dun, for assistance in various ways; also to Dr. K. C. Sahani, Forest Botanist at that same Institute, and Mr. B. V Shetty, Regional Botanist

at the Arid Zone Circle, Botanical Survey of India, Jodhpur, for assistance with the botanical nomenclature of trees. Finally, to Dr. N. S. Rathore and Mr. P. S. Chauhan, Jodhpur, for help with some of the diagrams.

SUMMARY

- 1. The process of initiation, progress and decline of the largest recorded epidemic (1953-54 eruption) of the Sal Defoliator, Lymantria mathura, in the Sub-Himalayas is described.
- 2. Though in normal years the defoliator is confined to barely half a dozen trees, in the 1953 eruption moths laid eggs, in the autumn of 1953, on as many as 185 different species; their list is given. However, the larvae survived only on 22 species.
- 3. The seasonal life-history was studied in the field as well as in the laboratory. Eggs are laid in small to large masses (each with about 50 to 1,200 eggs), which are covered by a thin layer of white material composed of long, thin microscopic hairs of a characteristic shape. There are five moults and six larval stages. In the Western Sub-Himalayas there are two annual generations —a first or summer generation (April to October) and a second or overwintering generation (September to June). The first generation eggs are laid from mid-April to mid-June, and hatch in 3 to 4 weeks. The second generation eggs are laid in autumn (early September to mid-October), then enter a diapause (with the embryo fully formed) and overwinter until they hatch in the following spring (February to early April).
- 4. The caterpillars have practically no predators, but are subject to fairly heavy parasitization by hymenopterous parasites. Both larvae and pupae are subject to serious attack by a polyhedral virus disease which spreads rapidly.
- 5. A precisely timed nocturnal feeding and "migratory" rhythm, which may be circadian, in mature caterpillars is described. The caterpillars rest during the day on tree trunks in large masses. At dusk they crawl up to the tree crown, feed there throughout the night and descend at dawn.
- 6. Just before the start of the upward march, and occasionally en route, caterpillars undergo, for a minute or two, a characteristic turning and twisting of the body.
- 7. The average speed of upward movement, including halts, is about 65.5 cm per minute; the downward movement is faster.
- 8. Three main colour forms are found in the mature caterpillars: a grey-white type which preponderates (66%), a dark, blackish-brown

- type (23%) and an intermediate type (11%). These types occur in mixed groups on tree trunks.
- 9. The caterpillars sit still in masses on tree trunks throughout the day, and move only at night. The dorsal and lateral colours perfectly match the background bark, making detection difficult even at short distances of a couple of metres. As a result, there are no bird or other vertebrate predators.

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APPENDIX

List of plants on which egg were laid by Lymantria mathura in the Western Sub-Himalayas (New Forest Estate and other forests in the Doon Valley, Uttar Pradesh, altitude 610 m) during the population eruption of September-October 1953.

(1) Number of trees on which eggs- masses were seen and counted are mentioned within brackets. (2) Degree of preference (for egg-laying) was grouped into three classes, as based on the average number of egg-masses per tree, as follows:—

Small (S): Below 10 egg-masses per tree.

Moderate (M): 10-40 ,, ,,

Great (G): Above 40 ,, ,,

Family (1) ANACARDIACEAE

- 1. Lannea grandis (Donnat) Engl. (1), S.
- 2. Mangifera indica Linn. (5), M. Mango.
- 3. Rhus lancea Linn. f. (1), S.
- 4. Schinus dependens Orteg. (1), S.
- 5. Schinus terebinthifolius Raddi (2), S.
- 6. Sclerocarya birroea Hoechst. (1), S.
- 7. Semecarpus anacardium Linn. f. (1), S.
- 8. Spondias axillaris Roxb. (1), S.

Family (2) ANONACEAE

9. Uvaria hamiltonii Hook. f. & Th. (2). S.

Family (3) APOCYNACEAE

- 10. Alstonia scholaris R. Br. (1), S.
- 11. Thevetia neriifolia Juss. (4), S.

Family (4) BIGNONIACEAE

- 12. Jacaranda brasiliensis Pers. (1), S.
- 13. Jacaranda ovalifolia R. Br. (5), M.
- 14. Kigelia pinnata DC. (1), S.
- 15. Millingtonia hortensis Linn. (1), S. Indian Cork-tree.
- 16. Stereospermum chelonoides DC. (1), S.
- 17. Stereospermum suaveolens DC. (1), S.
- 18. Tecoma argentea Bureau & K. Sch. (2), S.

Family (5) Boraginaceae

19. Cordia myxa Linn. (1), S. Lasorā.

Family (6) BURSERACEAE

- 20. Boswellia serrata Roxb. (1), S. Salai.
- 21. Protium serratum Engl. (syn. Burserra serrata Wall. ex Colebr.) (1), S.

Family (7) CASUARINACEAE

- 22. Casuarina cunninghamiana Miq. (5), M.
- 23. Casuarina equisetifolia Forst. (5), S. Casuarina.

Family (8) CELASTRACEAE

24. Elaeodendron glaucum Pers. (several), S. (Noticed in Thangaon forest near Dehra Dun.)

Family (9) Combretaceae

- 25. Anogeissus leiocarpa Guill. & Perr. (2) S.
- 26. Terminalia arjuna Bodd. (2), M. Arjun.
- 27. Terminalia belerica Roxb. (1), S. Baherā.
- 28. Terminalia chebula Retz. (1), S. Myrabolan tree.
- 29. Terminalia citrina Roxb. (1), S.
- 30. Terminali paniculata W. & A. (1), S.
- 31. Terminalia tomentosa W. & A. (3), S. Sain.

Family (10) Coniferate

- 32. Cupressus arizonica Greene (2), M.
- 33. Cupressus cashmiriana Royle (2), M.
- 34. Cupressus torulosa Don. (2), M. Himalayan cypress.
- 35. Juniperus procera Hoechst (2), S.
- 36. Pinus caribaea Mor. (3), S.

- 37. Pinus longifolia Roxb. (5), S. Chir pine, chir, chil.
- 38. Pinus merkusii Jungh & de Vriese (1), S. Tenasserim pine.
- 39. Pinus thunbergi Parl. (1), S.
- 40. Podocarpus gracilior Pilger (2), S.
- 41. Taxus baccata Linn. (5), S.

Family (11) CORNACEAE

42. Marlea begoniaefolia Roxb. (2), S.

Family (12) DILLENIACEAE

43. Dillenia indica Linn. (3) S.

Family (13) DIPTEROCARPACEAE

44. Shorea robusta Gaertn. f. (5), G. Sāl.

Family (14) EBENACEAE

45. Diospyros embryopteris Pers. (1), S.

Family (15) EUPHORBIACEAE

- 46. Aleurites fordii Hemsl. (5), S.
- 47. Bischofia javanica Blume (1), S. Kaen.
- 48. Breynia rhamnoides Muell. Arg. (1), S.
- 49. Macaranga sp. (5), S.
- 50. Mallotus philippinensis Muell. Arg. (1), S. Rohini.
- 51. Manihot tweediana Muell. Arg. (1), S.
- 52. Putranjiva roxburghii Wall. (2), S.
- 53. Sapium sebiferum Roxb. (1), S. Chinese tallow tree.

Family (16) FLACOURTIACEAE

- 54. Gynocardia odorata R. Br. (1), S.
- 55. Oncoba spinosa Forsk. (1), S.

Family (17) GNETACEAE

- 56. Araucaria cookii R. Br. (1), M.
- 57. Araucaria cunninghamii Ait. (5), M.

Family (18) GRAMINEAE

- 58. Dendrocalamus giganteus Munro (12 culms), M.
- 59. Dendrocalamus strictus Nees (3), S.

Family (19) GUTTIFERAB

60. Mesua ferrea Linn. (1), S.

Family (20) HYPERICINEAE

61. Cratoxylon polyanthum Korth. (1), S.

Family (21) JUGLANDACEAB

62. Pterocarya stenoptera DC. (2), S.

Family (22) LAURACEAE

63. Cinnamomum camphora Nees & Eberm. (1), G. Japan or Formosa camphor tree.

Family (23) LEGUMINOSAE

Subfamily (a) Caesalpineae

- 64. Acrocarpus fraxinifolius Wight (3), S.
- 65. Bauhinia anguina Roxb. (6 shoots), S.
- 66. Bauhinia galpini N. E. Br. (1), S.
- 67. Bauhinia hookeri F. Muell. (1), S.
- 68. Bauhinia kurzii Urban (1), S.
- 69. Bauhinia pubescens DC. (2), S.
- 70. Bauhinia purpurea Linn. (2), S.
- 71. Bauhinia regulosa Wedd. (5), S.
- 72. Bauhinia retusa Ham. (1), S. Kanlā.
- 73. Bauhinia variegeta Linn. (4), S. Kachnār.
- 74. Caesalpinia sappan Linn. (1), S. Sappan wood.
- 75. Cassia ferruginea Schrad. ex DC. (1), S.
- 76. Cassia fistula Linn. (5), S. Amaltās.
- 77. Cassia glauca Lam. (1), S.
- 78. Cassia javanica Linn. (5), S.
- 79. Cassia nodosa Ham. (1), S.
- 80. Cassia spectabilis DC. (2), S.
- 81. Gleditschia sp. (1), S.
- 82. Peltophorum africanum Sond. (2), S.
- 83. Peltophorum vogelianum Walp. (2), S.
- 84. Poinciana regia Bojer (3), S. Gold mohur.

Subfamily (b) Mimoseae

- 85. Acacia arabica Willd. (3), M. Babul.
- 86. Acacia auriculiformis A. Cunn. (4), S.
- 87. Acacia catechu Willd. (1), M. Cutch tree, khair.
- 88. Acacia confusa Merr. (5), S.
- 89. Acacia eburnea Willd. (1), S.
- 90. Acacia modesta Wall. (1), S.
- 91. Albizzia chinensis (Osbeck) Merr. (syn. A. stipulata Boir) (2), S. Kalā siris.
- 92. Albizzia procera Benth, (3), S. Safed siris.
- 93. Enterolobium contortisiliquum (Vell.) Morong (syn. E. tembouva Mart.) (2), M.
- 94. Parkia roxburghii G. Don. (1), S.
- 95. Xylia dolabriformis Benth. (1), S. Ironwood of Burma.

Subfamily (c) Papilionateae

96. Butea monosperma (Lam.) Ktze. (syn. B. frondosa Koen. ex Roxb.) (2), S. Dhak, palas.

- 97. Dalbergia latifolia Roxb. (5), S. Indian rosewood, blackwood.
- 98. Dalbergia sis soo Roxb. (5), M. Shisham, sissu.
- 99. Derris robusta Bth. (1), S.
- 100. Erythrina arborescens Roxb. (1), S.
- 101. Erythrina indica Lam. (1), S. Indian coral tree.
- 102. Erythrina suberosa Roxb. var. glabrescens Prain (5), S.
- 103. Lonchocarpus nitidus Benth. (1), S.
- 104. Milletia auriculata Baker (1), S.
- 105. Milletia tatraptera Kurz. (1), S.
- 106. Mundulea suberosa Bth. (2), S.
- 107. Ougenia dalbergioides Benth. (2), S. Sāndan.
- 108. Tipuana speciosa Benth. (1), M.

Family (24) LYTHRACEAE

- 109. Duabanga sonneratioides Ham. (1), S.
- 110. Lagerstroemia flos-reginae Retz. (4), S.

Family (25) MAGNOLIACEAE

- 111. Michelia champaca Linn. (2), S. Champak.
- 112. Michelia figo (Lour.) Spreng. (syn. M. fuscata Blume) (2), S.

Family (26) MALPIGHIACEAB .

113. Zyrosnima crassifolia H. B. & K. (2), S.

Family (27) MALVACEAE

- 114. Bombax insigne Wall. (1), S.
- 115. Bombax malabaricum DC. (=Salmalia malabarica), (4), S. Cotton trees simal.
- 116. Chorisia crispiflora H. B. & K. (1), S.

Family (28) MELIACEAE

- 117. Ammora rohituka W. & A. (2), S. Sohāgā.
- 118. Cedrela toona Roxb. (5), G. Tun, toon, red cedar.
- 119. Chloroxylon switenia DC. (3), S. Satinwood.
- 120. Dysoxylum binectariferum Hook. f. (1), S.
- 121. Heynea trijuga Roxb. (2), S.
- 122. Melia azedarach Linn. (2), S. Bakain, drek, Persian lilac.
- 123. Melia composita Willd. (2), S.

Family (29) MORINGACEAB

- 124. Moringa concanensis Nimmo (1), S.
- 125. Moringa pterygosperma Gaertn. (2), S. Sanjnā.

Family (30) MYRTACEAE

- 126. Callistemon viminalis (Solaud) (5), S. Cheel.
- 127. Callitris glauca Lam. (2), S.
- 128. Eucalyptus deglupta Bl. (1), S.

- 129. Eucalyptus resinifera Sm. (2), S.
- 130. Eucalyptus rostrata Schlecht. (5), S.
- 131. Eucalyptus torelliana F. Muell. (2), S.
- 132. Eugenia grandis Wight. (1), S.
- 133. Melaleuca ericifolia Sm. (1), S.
- 134. Melaleuca styphelioides Sm. (1), M.
- 135. Psidium guajava Linn. (2), M. Guava.
- 136. Syzygium cumini Linn (syn. Eugenia jambolana Lam. (3) G. Jamun, black plum.

Family (31) PALMEAE

- 137. Caryota mitis Lour. (3), S.
- 138. Caryota urens Linn. (5). S. Indian sago palm.
- 139. Phoenix sylvestris Roxb. (5). M. Wild date palm, khajur.

Family (32) PANDANACEAB

140. Pandanus furcatus Roxb. (2), S.

Family (33) RHAMNACEAE

- 141. Hovenia dulcis Thumb. (1), M.
- 142. Zizyphus incurva Roxb. (1), S.

Family (34) ROSACEAE

- 143. Eriobotrya japonica Lindl. (1), S.
- 144. Prunus communis Huds. (4), S.
- 145. Stranvaesia glaucescens Lindl. (1), S.

Family (35) RUBIACEAB

- 146. Adina cordifolia Hook. (5), S. Haldu.
- 147. Anthocephalus cadamba Miq. (5), M. Kadam.
- 148. Gardenia spetulifolia Stapf. & Hutch. (1), S.

Family (36) RUTACEAE

- 149. Aegle marmelos Correa (1). G. Bel.
- 150. Citrus decumana Linn. (1), S. Chakotra.

Family (37) SALICINEAE

151. Salix babylonica Linn. (1), S.

Family (38) SANTALACEAB

152. Santalum album Linn. (2), S. Sandalwood.

Family (39) SAPINDACEAE

- **153.** Acer negundo Linn. (1), S.
- 154. Acer oblongum Wall. (5), S.
- 155. Aesculus punduana Wall. (syn. A. assamica Griff.) (1), S.

- 156. Litchi chinensis Camb. (syn. Nephelium litchi Camb.) (5), S. Lichi.
- 157. Sapindus drumondii Hook. & Arn. (1), S.
- 158. Sapindus mukorossi Gaertn. (1), S.

Family (40) SAPOTACEAE

159. Madhuca longifolia (Koenig) MacBride var. latifolia (Roxb.) Chev. (syn. Bassia latifolia Roxb.) (1), S. Mohwa.

Family (41) SIMARUBACEAB

160. Ailanthus excelsa Roxb. (2), S. Maharukh.

Family (42) SOLANACEAB

161. Dolichandrone falcata Seem. (3), S.

Family (43) STERCULIACEAE

- 162. Eriolaena hookeriana W. & A. (1), S.
- 163. Pterospermum acerifolium Will. (2), S.
- 164. Sterculia alata Roxb. (5), S.
- 165. Sterculia colorata Roxb. (4), S.
- 166. Sterculia pallens Wall. (1), S.
- 167. Sterculia villosa Roxb. (2), S.

Family (44) Ternstroemiaceae

168. Schima wallichii Choisy (5), S.

Family (45) TILIACEAB

- 169. Grewia subinaequalis DC. (syn. G. asiatica Mast, in part, nec. Linn.) (1), S.
- 170. Grewia sp. (1), S. (In Thangaon forest near Dehra Dun.)

Family (46) URTICACEAE

- 171. Artocarpus integrifolia Linn. f. (3), M.
- 172. Artocarpus lakoocha Roxb. (1), S. Barhal.
- 173. Ficus bengalensis Linn. (2). S. Bar, bargad.
- 174. Ficus racemosa Linn. (syn. F. glomerata Roxb.) (1), G.
- 175. Ficus infectoria Roxb. (1), S.
- 176. Ficus religiosa Linn. (1), G. Pipal.
- 177. Maclura pomifera Schnied. (1), S.
- 178. Morus alba Linn. (2), M. Mulberry.

Family (47) VERBENACEAE

- 179. Caryopteris mastacanthus Sch. (1), S.
- 180. Litharexylum quadrangulare Jacq. (1), S.
- 181. Premna mucronata Roxb. (syn. P. latifolia Roxb.) (1), M. Bakar.
- 182. Tectona grandis Linn. (5), S. Teak.
- 183. Tectona hamiltoniana Wall. (3), S.
- 184. Vitex negundo Linn. (1), S.
- 185. Vitex peduncularis Wall. (1), S.