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THE LIFE-HISTORY OF *ACTIAS MAENAS* (SATURNIIDAE)[1]

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ABSTRACT. Broods of the Southeast Asian *Actias maenas* Doubleday (=*A. leto*) were reared in Germany and South Carolina utilizing stock from West Malaysia and northern Sumatra. Larvae preferred *Liquidambar styraciflua* and *Rhus* spp. among a variety of hostplants offered. Larval development at 23–28°C required 31 to 40 days; the pupal stage lasted 12 to 15 days. The first instar larva is orange with a black head and black marking on the tergum. The mature larva (fifth instar) is dark lime green with a brown head and green spiny scoli, with yellow bands on the posterior edge of abdominal segments 2–7. Females fly prior to mating. Mating commences 1–2 h before sunrise and lasts only a few hours. The species appears to be polyvoltine, without pupal diapause. Some larvae were killed by a disease caused by the microsporidian *Nosema*.

ZUSAMMENFASSUNG. Die südostasiatische *Actias maenas* Doubleday (=*A. leto*) wurde in Deutschland und South Carolina (U.S.A.) gezüchtet; das Zuchtmaterial stammte aus West Malaysia und Nordsumatra. Die Raupen bevorzugten *Liquidambar styraciflua* und *Rhus* spp. unter den angebotenen Futterpflanzen. Die larvale Entwicklungszeit bei 23–28°C dauerte 31 bis 40 Tage, das Puppenstadium 12 bis 15 Tage. Das erste Raupenstadium ist orange mit schwarzen Kopf und schwarzer Zeichnung. Die ausgewachsene Raupe (5. Stadium) ist dunkel gelbgrün mit braunem Kopf und grossen grünen dornigen Sternwarzen, am Hinterrand der Abdominalsegmente 2 bis 7 mit gelben Streifen. Die Weibchen fliegen vor der Begattung. Die Paarung findet 1–2 Stunden vor Sonnenaufgang statt und dauert nur wenige Stunden. Die Art dürfte polyvoltin sein, ohne Puppendiapause. Etliche Raupen wurden durch Darmkrankheiten getötet, ausgelöst durch *Nosema*-Erreger.

Actias maenas Doubleday (1847) has been known for well over a century and is very popular with collectors, yet the larval stages of this moth are not well known. The species ranges from sub-Himalayan regions of northeastern India through most of the Southeast Asian mainland and on the Greater Sunda Islands, a distribution of more than 4000 km. The biotope covers diverse biomes including tropical rainforest, paratropical rainforest, and notophyllous broad-leaved evergreen forest (Wolfe, 1979).

Adults exhibit striking sexual dimorphism; males (Fig. 1) are bright yellow with brown markings, whereas females (Fig. 2) are light green.

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[1] No. 4 of the series "Contributions to the knowledge of the Saturniidae" by the senior author.
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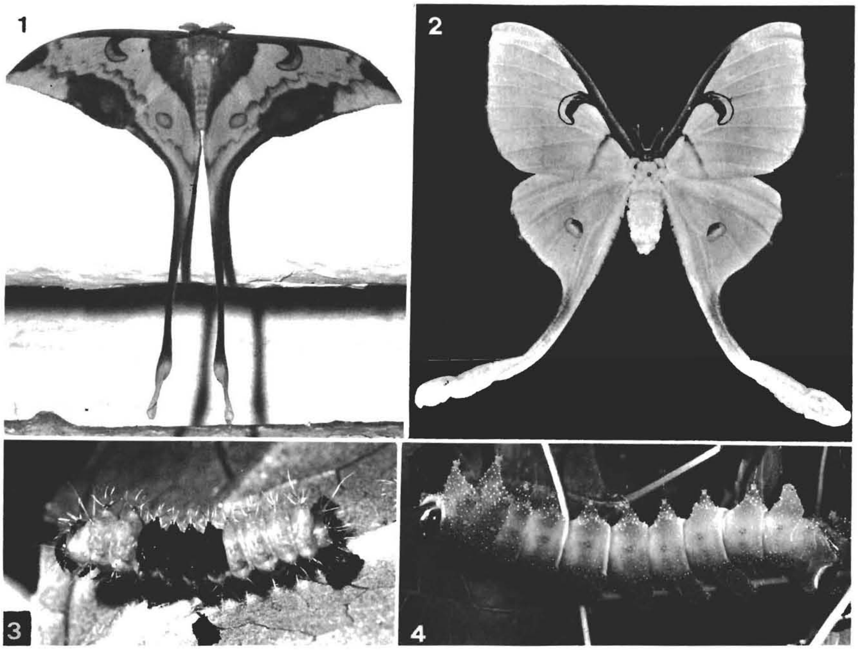

FIGS. 1–4. *Actias maenas*. **1**, male, live specimen in natural repose; **2**, female, pinned specimen; **3**, first instar larva just prior to molting into second instar; **4**, mature larva feeding on sweetgum.

The insect was recently characterized morphologically by Arora and Gupta (1979), including drawings and a detailed description of the male genitalia and wing venation. Narang and Gupta (1981) reported on cytological investigations of this saturniid. Despite these recent studies, a considerable amount of taxonomic confusion persists with *Actias maenas*. For examples, (1) the junior synonym *leto* (Doubleday) continues to appear commonly on lists of dealers and labels of specimens; (2) the genus has been excessively split, with even the recent Indian authors cited above using the generic name *Sonthonnaxia* Watson, whereas other authors (Bouvier, 1936; Allen, 1981; Barlow, 1982) considered this large Asiatic species to belong to the African genus *Argema* Wallengren; (3) the so-called insular subspecies or forms appear to us to be either distinct species (e.g., *isis* Sonthonnax from Celebes, and *ignescens* Moore from the Andamans) or simply subjective synonyms of *A. maenas* (e.g., *saja* van Eecke from Java and Sumatra, and *recta* Bouvier from Sumatra). Satisfactory resolution of these problems must await a modern revision of the genus.

To date virtually no comparative studies have been published on the pre-imaginal instars within the genus *Actias*. The early stages of *A. maenas* were described by Roepke (1918), and Packard (1914, pl. 96) figured the pupa and cocoons. Gardiner (1982, pl. 8) published a color photograph of a mature larva. In the present paper the structure and behavior of the pre-imaginal stages are described in greater detail and compared with related species. Moreover, we present information on courtship behavior, hostplant relationships, diseases, and parasitism.

Rearing Observations

In May 1982 the senior author received six cocoons of this species from Tapah, Perak, West Malaysia. With adults emerging from these cocoons, a mating was achieved and part of the eggs was sent to the junior author. Rearing was successful in both Germany and South Carolina. Additionally, another brood was reared by the senior author during the winter of 1982–1983 utilizing stock from northern Sumatra, Indonesia. Observations and descriptions below are based on the Malaysian material except where otherwise noted.

Emergence of the adults was in the evening in Germany, within a few hours after sunset. In South Carolina, some adults also emerged within 2 hours after sunset, while others of both sexes emerged between 0200 and 0400 h (Eastern Standard Time). Adults have minimal difficulty pushing out of the flimsy cocoons. Wing expansion is complete within 45 min after emergence. During expansion the tails do not begin to elongate until after the forewings have completely expanded. Both sexes are easily excitable, flapping vigorously on the ground or bottom of the cage after being disturbed. The long tails on live specimens are surprisingly flexible and are not easily broken off. In natural resting position these tails are held parallel or nearly so (see Fig. 1), while tails of specimens of *Argema* are frequently crossed in repose. On a vertical substrate the moths rest at an angle, i.e., the longitudinal axis of the body is positioned parallel against the substrate, but is off 20° or more from the vertical, either to the right or the left.

Females fly after wings have hardened but before emitting pheromone, generally shortly after sunset. This character is an unusual one among Saturniidae where females of most species emit pheromone and mate prior to their first flight. However, this character is probably normal for the *Actias* group in general; the junior author observed this in *A. luna* (L.) in nature, and Marten (1955) reported the same behavior with *Graellsia isabellae* (Graëlls) in Spain. Mating probably occurs in treetops with these insects. Several hours after the virgin flight, females emit pheromone. In Germany, the first pairing occurred between 0100 and 0300 h (MEZ)[3] in a cage outdoors. Conditions during

[3] mitteleuropäische Zeit—Central European Time.

mating were as follows: cloudless, temperature 15.0°C, relative humidity 72%. The pair remained united until after 0700 h. In South Carolina in early August, an F_2 pairing occurred between 0430 and 0500 h (EST), and lasted until ca. 0800 h. The different mating times observed in Germany and South Carolina actually agree in terms of their relation to respective times of sunrise.

Both authors reared larger numbers of *Actias sinensis heterogyna* Mell alongside the broods of *A. maenas,* and both species demonstrated the same respective mating times in Germany and South Carolina, i.e., covering the two hours on either side of sunrise. Attempts to hybridize *A. maenas* with the much smaller *A. sinensis heterogyna* were not successful. We were unable to hand-pair either species (including inter- and intraspecific matings). In South Carolina adults of both species were present in one large cage, and females of both species emitted pheromone simultaneously, but males of both species mated only with conspecific females.

The original female in Germany deposited ca. 170 ova during the first two nights, and laid only ca. 30 eggs total during the following three nights. Most of the last deposited eggs were infertile, as is normal for Saturniidae (cf. Miller & Cooper, 1977). Incomplete data on fecundity recorded for an F_2 female in South Carolina were very similar to the above. In both cases females were killed with a small number of eggs remaining in their abdomens in order to preserve the good condition of these specimens for collections.

Hostplants in nature given by Arora and Gupta (1979) are *Turpinia sphaerocarpa* Hassk. (=*T. pomifera*), Staphyleaceae, and *Schima wallichii* (DC.) Korth., Theaceae.[4] Barlow (1982) cited *Averrhoa bilimbi* L., Oxalidaceae, as a host. A specimen from Bogor, Java, in the Rijksmuseum van Natuurlijke Historie (Leiden, Netherlands) was reared on *Adinandra dumosa* Jack, Theaceae. Roepke (1918) reared his material in Java on *Canarium*, Burseraceae. The moth has also been reared on *Eucalyptus gunnii* Hooker, Myrtaceae (Gardiner, 1982). Since none of these plants were available to us, several alternatives were offered to the larvae. The food which appeared to be most preferred was sweetgum (*Liquidambar styraciflua* L., Hammelidaceae), although larvae in all instars freely accepted staghorn sumac[5] (*Rhus typhina* L., Anacardiaceae) in Germany, and winged sumac (*R. copallina* L.), smooth sumac (*R. glabra* L.), and poison ivy (*R. radicans* L.) in South Carolina. Several species of oak (*Quercus*, Fagaceae) were accepted as well, the evergreen species of which are probably the best choice for rearing during the northern winter. First instar larvae also fed reluc-

[4] The spelling, synonymy, and family-classification of plants listed follow the work of Backer and Bakhuizen van den Brink (1963–1968).

[5] The North American trees sweetgum and staghorn sumac are grown as ornamentals in Germany.

TABLE 1. Development of F_1 brood of *Actias maenas* on sweetgum in Germany (23–28°C) and South Carolina (25–28°C). Mating occurred 31 May 1982.

	Eclosion	Molt 1	Molt 2	Molt 3	Molt 4	Spinning
Germany	10–14 June	15–18	20–24	26–30	2–6 July	17–23
South Carolina	12–13 June	17–18	22– —	28–30	2–5 July	13–17

tantly on rose (*Rosa*, Rosaceae), black walnut (*Juglans nigra* L., Juglandaceae), and *Staphylea colchica* Stev., Staphyleaceae, although both authors reared larvae mainly on sweetgum. Some of these other plants might be utilized successfully by rearers where sweetgum and sumac are not available. *Actias maenas* has been reared in the Amsterdam Zoological Garden (van Eecke, 1913; W. Hogenes, pers. comm.), but no records of which hostplants were used could be located.

The hostplants accepted in nature and captivity by *Actias maenas* coincide with those known for related species. *Argema mimosae* (Boisduval) from Africa feeds on walnut and certain Burseraceae and Anacardiaceae (Pinhey, 1972), and *Argema mittrei* (Guérin-Méneville) from Madagascar accepts several species of *Rhus* (Villiard, 1969) and certain Myrtaceae (Pinhey, 1972). *Actias sinensis heterogyna* from Taiwan, partially sympatric with *A. maenas*, feeds on *Liquidambar formosana* Hance in nature (Mell, 1950) and *L. styraciflua* in captivity (Nässig, 1980). Walnut, oak, and sweetgum are well-known hosts of the Nearctic *Actias luna*, and are accepted by the Asiatic *A. selene* (Hübner) as well. Sweetgum is also used in nature in Mexico by *Actias truncatipennis* Sonthonnax (Beutelspacher, 1978).

Newly hatched larvae are very active and move quickly about in the rearing container. Larvae show minimal tendency to congregate, even in the first instar. The resting position is with the anterior end of the body held free of the leaf or stem, the typical "sphinx" position for Sphingidae and most Saturniidae. Larval development was rapid under temperatures of 23–28°C, the time from eclosion of eggs to spinning of cocoons being ca. 31 to 40 days (Table 1). Males complete development a few days more rapidly than sibling females, both in the larval and pupal stages, because they are smaller. Equally good results were achieved by rearing in open air (Nässig) and under plastic bags (Peigler) to ensure high relative humidity; both of us reared all larvae indoors on cut food with stems inserted into water.

Structurally, larvae of *A. maenas* are similar to other species of *Actias* and *Argema*. The first instar is orange as in *A. selene* from Bhutan, *A. sinensis heterogyna*, *A. artemis*? (Bremer) from South Korea, and *Argema mimosae* (only *A. luna* is green in the first instar).

In the second instar the body of *A. maenas* becomes yellowish green as in the case of *A. artemis*?; *A. selene* and *A. sinensis heterogyna* remain orange. The third instar is green for all species. The subspiracular yellow stripe of the mature larva of *A. selene* and *A. artemis*? is absent in *Argema* and all other species of *Actias* mentioned above. Mature larvae of *A. maenas* look much more like those of *Argema* than any *Actias* which we have seen. The dark green integument with contrasting short whitish setae are seen in *Argema mittrei* (Villiard, 1969), while the elongated fleshy extensions of the body which support the dorsal scoli are also present in *Argema mimosae* (Pinhey, 1972:pl. 1) and to a lesser degree in *A. selene*. All species of *Actias* and *Argema* for which the larvae are known have a single median dorsal scolus on abdominal segment 8, a character which easily separates the group from several similarly appearing larvae of *Saturnia* Schrank and allied genera in which a pair of dorsal scoli is present on abdominal segment 8.

In the later instars of *Actias maenas*, the scoli bear stout spines, especially the dorsal scoli. These possibly have mechanical defensive benefits, because they lack fluid secretions seen in several other saturniid caterpillars, e.g., *Saturnia pyri* [Denis & Schiffermüller] (Haffer, 1921). In the last three instars the ventral side is a darker green than the dorsal side, this providing a very effective camouflage known as countershading (de Ruiter, 1955).

Dupont and Scheepmaker [1936] stated that larvae of *Actias* reared in Java were very susceptible to disease, a problem also noted by Roepke (1918). All larvae of an F_2 brood in South Carolina succumbed to a disease before reaching the last instar. Of the four main types of pathogens infecting Saturniidae, *viz.* viruses, bacteria, fungi, and microsporidians, outlined by Jolly et al. (1979:61–66), the symptoms agreed with the latter. The pathogen belongs to the genus *Nosema* (Nosematidae). The symptoms include reduced feeding, lethargy, black spots on the integument, darker body color, and stunted growth. A large portion of the F_1 brood of larvae in Germany was also killed by an unidentified disease. Higher humidity is beneficial to Lepidoptera which are native to tropical rainforests, but unfortunately such conditions also promote disease.

Cocoons of *Actias maenas* are attacked in nature by one or more species of *Xanthopimpla* (Hymenoptera: Ichneumonidae) belonging to the *regina* species-group (Townes & Chiu, 1970). We were unable to locate other published records of parasitism for this moth.

Mature larvae spin cocoons among leaves of the hostplant or among dead leaves on the bottom of the cage. There appeared to be no preference in selection of a pupation site. In nature, presumably some

TABLE 2. Behavioral characteristics of *Actias maenas* considered to be of generic level.

First instar larvae move about rapidly
Larvae not gregarious, even in first instar
Pupa with spines on cremaster anchored into cocoon
Pupa frequently active
Females fly prior to emitting pheromone
Adults excitable at all times; copula is broken at slightest disturbance
Adults rest at angle on vertical substrate
Predilection for *Liquidambar* and Anacardiaceae as hostplants

cocoons are formed at ground level while others are spun high above the ground among living leaves. Freshly spun cocoons are white; the silk usually then turns light or dark brown. Most cocoons have small perforations as in the cocoons of *Actias selene, A. sinensis heterogyna*, and *Argema mimosae*. A few cocoons of *A. maenas* have less than five discernable perforations and occasionally none at all. Packard (1914) figured an imperforate cocoon alongside one with numerous perforations. The imperforate cocoon was also stated to be a 'valveless' cocoon, but we have not seen cocoons of *A. maenas* which lack the pre-formed exit at the anterior end. The hooked spines of the pupal cremaster are anchored into the posterior end of the cocoon. This undoubtedly facilitates the emerging moth when pulling itself out of the pupal shell. The active pupa is frequently heard rolling in the papery cocoon at any time during the pupal stage, especially when disturbed by an external stimulus (refer to Table 2).

Diapause of some species of *Actias* has been investigated. In general, photoperiod is the primary mechanism which maintains and terminates diapause in temperate species such as *A. luna* (Wright, 1970) and Japanese species (Miyata, 1974, 1976, 1977). *Actias maenas* is a tropical species however, the range of which crosses the Equator. *Actias sinensis heterogyna*, with a slightly more northern range, diapauses only rarely: only one female among ca. 100 pupae in Germany diapaused for six months at 6°C; short-day photoperiod, senescing hostplants, and lower temperatures during larval and pupal stages all failed to induce diapause in *A. s. heterogyna* (Nässig, 1980 and unpubl.; Mell, 1950). These data plus the rapid life cycles indicate that both *A. maenas* and *A. s. heterogyna* are polyvoltine in nature, notwithstanding the presence of a light-detecting "window" on the head of the pupa in each species (see Fig. 5). However, Bouvier (1936:254) indicated that *A. maenas* is bivoltine in northeastern India, a region where mild

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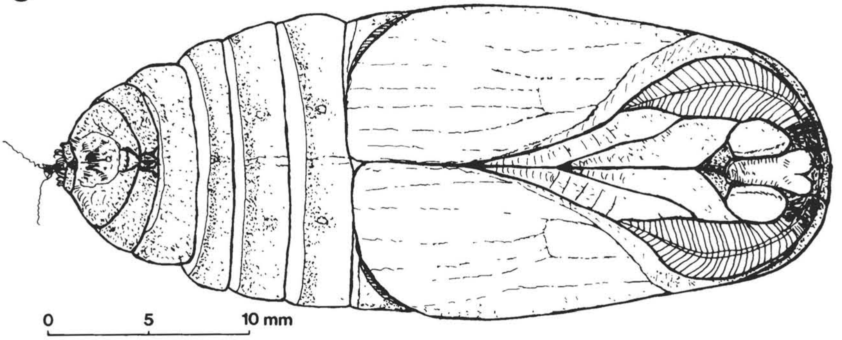

FIG. 5. *Actias maenas*, ventral view of male pupa. Note transparent "window" between eyes and base of antennae, and strands of silk from cocoon attached to cremaster.

winters occur (Wolfe, 1979). No seasonal forms are known for adults of either species.

Descriptions of Immature Stages

The following descriptions are based on living material, freeze-dried larvae, and color transparencies. The minor differences noted between material from West Malaysia and Sumatra are not believed to be taxonomically significant. The photographs and drawing in this paper were all made by the senior author.

Ovum. Length 2.5 mm, width 2.1 mm, height 1.6 mm. (Sizes of eggs from Malaysian and Sumatran material are the same, but Roepke (1918) cited smaller measurements for Javanese eggs.) Coloration whitish brown. Irregular areas of chorion opaque or translucent. Chorionic sculpturing evenly reticulate, average diameter of meshes 0.02 mm. Partially coated with brown secretion for affixing egg to substrate.

Larva. First instar (Fig. 3). Head glossy black, 1.1 mm in diameter. Integument orange; dorsal and lateral area of abdominal segments 1 to 4 black. Thoracic legs, prolegs, and posterior edge of anal plate all black. Scheme of implantation of scoli in six longitudinal rows, with two rows each of dorsal, subdorsal, and lateral, excepting single median dorsal scolus on abdominal segment 8. (Roepke's (1918) statement that there are only four rows of scoli we believe to be erroneous.) Scoli not prominent, concolorous with integument, each with 4–6 short white primary setae, longer ones on thoracic and subspiracular scoli. Larval length reaching more than 1 cm.

Second instar. Head glossy dark brown, lighter frons and clypeus, ca. 2.5 mm in diameter. Integument light yellowish green, with irregular tiny white granulations, each bearing seta. Thoracic legs and dorsal portion of prolegs black to dark brown. Prothoracic plate in some individuals with an irregular black patch, more prominent in Sumatran material. Anal plate dark brown with yellow border. Subspiracular line yellow, connecting subspiracular scoli, less distinct in Sumatran material. Bases of scoli yellow, distally becoming orange or red in dorsal and subspiracular rows, yellow in lateral rows. Each scolus with single black seta arising from center, and 4–7 radial black spines. Larval length reaching 2 cm.

Third instar. Head glossy brown, lighter frons and clypeus, 3.5 mm in diameter. Integument dark lime green, with numerous contrasting white granulations, each with seta. Thoracic legs dark brown. Prolegs dark gray. Prothoracic plate green, concolorous with integument. Anal plate light brown with ca. 20 small black spots, anterior edge yellow; anal prolegs dark brown with anterior edge yellow. Spiracles green, concolorous with integument. Subspiracular stripe yellow. Scoli yellow, becoming green distally, in Sumatran material sometimes all but largest scoli remaining yellow or even orangish with basal red ring, as in other species of *Actias*. Larval length ca. 3.2 cm.

Fourth instar. Same as third instar except head 4.0–4.5 mm in diameter, subspiracular stripe disappearing, scoli all becoming larger, and fleshy extensions of body supporting scoli becoming more prominent. Larval length ca. 6 cm.

Fifth instar (Fig. 4). Same as third and fourth instars except head 5–7 mm in diameter, spiracles dark grayish yellow, scoli each with 4–10 central and radial black spines 0.5–1.5 mm long, best developed on dorsal pairs of meso- and metathoracic scoli plus median caudal scolus (this scolus was lost on specimen figured due to an accident), and posterior edge of first seven abdominal segments with light yellow stripe. Larval length 9.5–10.5 cm.

Pupa (Fig. 5). Color dark brown. Antennal covers small, surrounded by leg covers. Head with transparent (whitish yellow) "window" between compound eye covers. Abdominal segments telescoped to small degree, pair of small protuberances on ventral side of segments 5 and 6 homologous to prolegs (cf. Mosher, 1916). Cremaster with several hooked spines. Length of male ca. 4 cm, female ca. 5 cm, width 1.5–2.0 cm (reared material being smaller than this).

Cocoon. Ovoid, irregular in shape. Length 5–6 cm, width 2.0–3.5 cm. Texture papery, spun between leaves. Coloration light brown with glossy sheen. Usually sparsely perforated. Pre-formed exit opening present at anterior end. Occasionally incomplete net-like inner cocoon is observed.

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