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OBSERVATIONS ON THE PHENOLOGY AND BIOGEOGRAPHY OF *THAUMETOPOEA JORDANA* (STAUDINGER) (LEPIDOPTERA: THAUMETOPOEIDAE)

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ABSTRACT

The biogeography of the processionary caterpillar genus *Thaumetopoea* is discussed, especially *T. jordana* (Staudinger) and its host *Rhus tripartita* (Bernard. da Ucria) Grande. Both are Saharo-Arabian elements found primarily in the Lower Jordan Valley of Israel and Jordan, the moth being apparently endemic to the region.

The biology and development time of the eggs, larvae, and pupae of *T. jordana* are given from field observations and laboratory rearing, under various constant temperatures as well as ambient conditions in the Coastal Plain of Israel. The adult flight period is about 85 days beginning in September/October and each female deposits a single cluster of eggs averaging 197 eggs. Incubation period is approximately six weeks. Larval development takes from 40—70 days at temperatures of 20—30°C and spans from October/November until late March. The 6—8 month period between pupation and emergence indicates a desert-adapted pupal diapause.

An encrytid wasp egg parasite, *Ooencyrtus* prope *masii* Mercet, and a tachinid fly larval parasite, *Palesisa nudioculate* Villeneuve, are reported.

INTRODUCTION

Staudinger (1894) first described *Cnethocampa (=Thaumetopoea) jordana* from specimens collected for him in Palestine by J. Paulus, from October 1 until November 3. There are specimens collected by Paulus near Jericho and the Dead Sea, in the collection of H. Bytinski-Salz (Tel Aviv). Aharoni (1912) reported finding moths in September and October in the Jordan Valley. Amsel (1933)

recorded this species in the mountains and Jordan Valley (Palestine) and he (1935) also collected two males on May 4, on the Allenby Bridge over the Jordan River.

Trought (1954) found and reared *T. jordana* from the Zerka River (the biblical Jabbok River) in Jordan. He captured adults, attracted to light, from September 29 until early November (also a few males in early May). He first recorded its host plant *Rhus tripartita* and gave some morphological description of eggs and larvae as well as behavioral notes on all stages. He bred larvae that pupated March 19-20 and the adult moths emerged from October 12 until November 29.

In the genus *Thaumetopoea* (10 species) the zoogeographic distribution of most species is Mediterranean with one Euro-Siberian

TABLE 1. Distribution and host plants of the species of *Thaumetopoea* (after Halperin, 1974)

Species	Distribution (Zoogeography)*	Host Plant
processionea (L.)	Portugal to N Turkey (Med/ES)	*Quercus*
pityocampa (Schiffermüller)	Europe (south of LeHavre-Bulgaria line) (Med/ES)	*Pinus, Cedrus, Abies, Picea*
wilkinsoni Tams	Turkey, Cyprus, Syria,Lebanon, Israel (Med)	*Pinus, Cedrus*
undescribed species	Turkey (SW Anatolia) (Med/IT)	*Cedrus*
pinivora (Treitschke)	Baltic countries (ES)	*Pinus*
bonjeani (Powell)	Morocco (Med)	*Cedrus atlantica* Manueti
solitaria (Freyer)	Greece to Iran, Israel (Med/IT)	*Pistacia*
jordana (Staudinger)	Jordan, Israel (SA)	*Rhus tripartita*
cheela Moore	NW India (=Pakistan) (IT)	*Rhus cotinus* L. (=*Cotinus coggyria* (Scop.)
herculeana (Rambur)	Portugal to Libya (Med)	*Helianthemum, Cistus,? Erodium*

**Med = Mediterranean; ES = Euro-Siberian; IT = Irano-Turanian; SA = Saharo-Arabian.*

species, one Saharo-Arabian species and one Irano-Turanian species. A few species extend into adjacent parts of the Euro-Siberian or Irano-Turanian (southern Asia to Iran, etc.) regions (see Table 1).

The *Thaumetopoea* species have an interesting range of host plants with five species feeding on Pinaceae *(Pinus* and/or *Cedrus)*, three species on Anacardiaceae *(Rhus* or *Pistacia)*, one species on Fagaceae *(Quercus)*, and one species on Cistaceae *(Cistus* and *Helianthemum)* and questionably on a Geraniaceae *(Erodium)* (see Table 1).

The species in the genus *Thaumetopoea* have an interesting biology commencing with the egg clusters (containing several rows of eggs) that are laid on the branches or needles of the host and covered with a protective layer of scales from the posterior end of the female's abdomen and all oriented in one direction. The larvae hatch more or less simultaneously and proceed to feed together, in a processionary manner, on the leaves of the host throughout their larval life. Pupation takes place several centimeters beneath the ground surface inside of a cocoon and in one species in the larval tent.

METHODS

The distribution of *Rhus tripartita* in Israel was determined using existing literature, personal communication with botanists, and extensive fieldwork. The range of distribution of *T. jordana* in Israel was also established through field work by checking as many of the host plant populations as possible.

A population of *T. jordana* newly hatched (1-3 days) larvae were collected on November 21, 1977 in Wadi Qilt (Judean Desert, west of Jericho) and reared under constant laboratory conditions of 27°C, 65% relative humidity, and a 12 hour photoperiod, in Rehovot at the Faculty of Agriculture. Larvae collected on January 18, 1978 from Wadi Qilt were reared to adults under natural outdoor conditions at the Entomology Laboratory, Agricultural Research Organization, Ilanot. The fecundity of the adult females from this population was checked. Also on this date, and again on March 16, a survey in the field (W.Qilt) of the population percentage of eggs and different larval instars was made.

On September 28, October 21, November 8, and December 12, 1978, approximately 0.5 Km^2 was surveyed in W. Qilt (during a three hour period) for newly deposited egg clusters. All clusters recovered were brought to the laboratory (Ilanot) for rearing. The W. Qilt site was

also checked for summer adult emergence and new egg clusters on June 27, 1979. Eggs collected on October 21, 1978 were incubated under room conditions of Ilanot. Larvae hatching from these eggs were reared on leaves of *Schinus terebinthifolius* under constant temperature (in darkness) at 16°C; 20°C; 25°C; and 30°C. Eggs collected on November 8, 1978 were incubated (in darkness) at constant temperatures of: 10°; 15°; 20°; 25°; and 30°C and the hatching larvae were reared on *Schinus terebinthifolius* under outdoor conditions at Ilanot. Pupae were maintained indoors (in darkness) at constant temperatures of: 20°, 25°, and 30°C and also outdoors in cages with pots and boxes of soil at Ilanot.

RESULTS

Distribution of *T. jordana* and *R. tripartita*

Thaumetopoea jordana is a specific feeder on *Rhus tripartita* (Berhard. da Ucria) Grande. This plant has a relictual distribution in the steppes and deserts from western North Africa to Sudan and eastward to Jordan, Israel, Lebanon, and Syria; with occasional extensions into the Mediterranean garigue (Zohary, 1972; Post, 1932). Therefore, it has basically a Saharo-Arabian distribution with extension into the Mediterranean and Irano-Turanian regions. Locally, *R. tripartita* is known from: Sinai Mountains; North, Central and South Negev Desert; Dead Sea valley; Judean Desert; Lower Jordan Valley; and Samaria (Zohary, 1972- in part). Most populations of *R. tripartita* in Israel are isolated and usually few in number (less than ten plants - A. Danin, personal communication). There are exceptions to this where larger populations exist, for example in SW Sinai Mountains, Judean Desert, Lower Jordan Valley and Samaria. The largest populations of this plant in Israel are in the Judean Desert, especially in Wadi Qilt (the ancient route between Jerusalem and Jericho). Another very large population exists in the foothills and mountains of eastern Samaria.

We have discovered stages of *T. jordana* in the following areas of Israel: egg clusters, November 20, 1977 on several trees in En Gedi (Dead Sea); first and second instar larvae, December 17, 1977 20 Km. north of Jiftlik (Lower Jordan Valley); a single old egg cluster, early November at Yarhiv (E. Samaria); and very large populations (all stages) in the Judean Desert, especially Wadi Qilt and Nahal Og (Og in Hebrew = *Rhus*) beginning on October 21, 1977. It is this population, particularly in W. Qilt, on which we conducted biological studies of this processionary caterpillar.

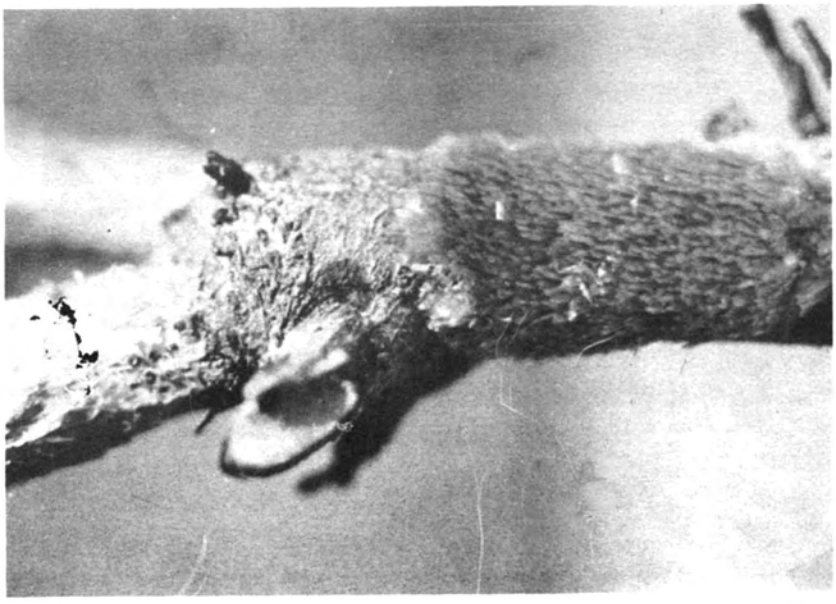

Fig. 1. *Thaumetopoea jordana*. An egg cluster covered with female abdominal scales (photo by D.G. Furth).

Fig. 2. *Thaumetopoea jordana*. Larvae in procession on *Rhus tripartita* (photo by J. Halperin).

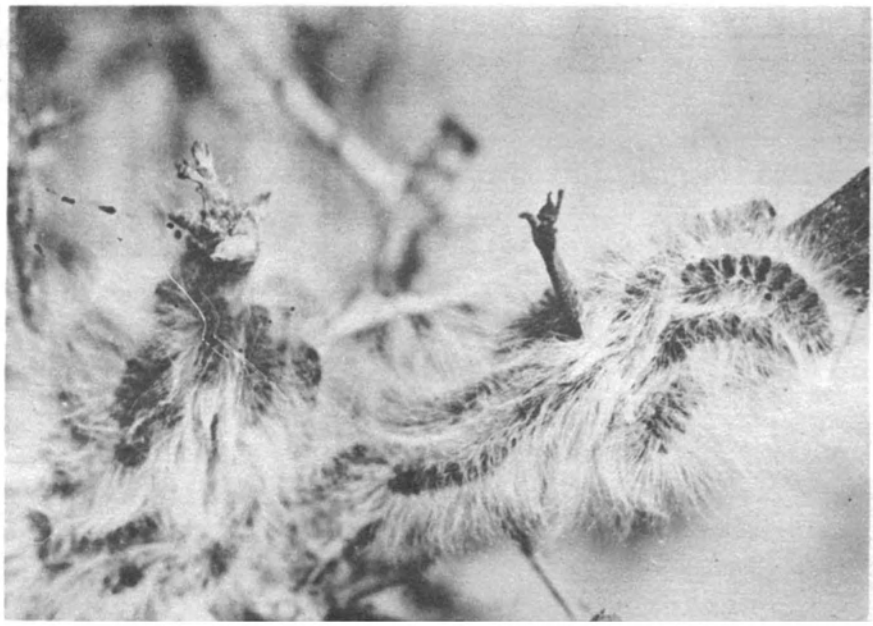

Fig. 3. *Thaumetopoea jordana*. Mass of final instar larvae. (photo by D.G. Furth).

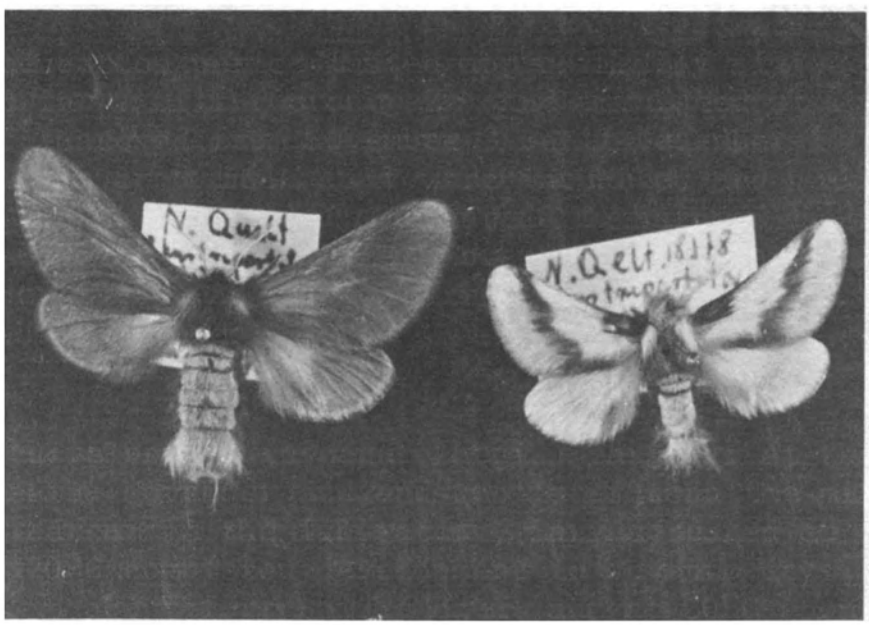

Fig. 4. *Thaumetopoea jordana*. Left = female; right = male (photo by Mrs. C. Sadowsky).

Biology of *Thaumetopoea jordana*

We found (during 1978) that the total range of the flight period is about 85 days (September 28 to December 12). It is noteworthy that the first egg cluster discovered in late September 1978 was deposited on one of the only bushes in the area with a significant amount of new leaves (the W.Qilt *R. tripartita* population is deciduous in late summer and early fall). The peak of the oviposition took place in W. Qilt during the first two to three weeks of October. The eggs were arranged in several rows, oviposited in masses or clusters, and covered with a layer of scales deposited on the eggs from the apex of the female's abdomen (Fig. 1). The number of eggs per field-collected cluster ranged from 105 to 258 with an average of 197. However, in those bred under laboratory, room, or outdoor conditions in 1977-78, the number of eggs ranged from 73-207 eggs (average 138) and in 1978-79 from 79-201 (average 136) per female. Each female lays only one cluster of eggs on the bark of the branches and it may remain there for several years after hatching. During the first year or two after hatching the scales covering the egg clusters also remain attached, but eventually after weathering they are sloughed off. The scales of the freshly deposited clusters have a slight but evident difference in color from those of the previous year. The fresh scales have a deep brown or reddish brown color, whereas those remaining from previous years are more bleached and have a light brown or tan color. This is quite evident when a fresh cluster is deposited beside an older one.

The incubation period lasted approximately six weeks. Those eggs collected in W. Qilt (October 21) and incubated at room temperature in Ilanot, hatched from November 3 until December 10. Those eggs collected on November 8 in W. Qilt were incubated and hatched as follows: 15°C and 16°C, no hatching; at 20°C, hatched from November 16 til December 5; at 25°C, hatched November 12-26; and at 30°C, hatched November 15-24. An egg parasite, *Ooencyrtus* prope *masii* Mercet (Encyrtidae) was recovered.

Larval development in nature begins earliest at the very end of October or early November and ends no later than the middle or latter half of March. In the laboratory, larvae reared at a constant temperature of 20°C completed development in seventy days, those at 25°C developed in about forty-eight days, and at 30°C about forty days is required for development. A field collected population of first instars (1-3 days old) took 60-68 days until pupation under lab conditions of 27°C, 12 hour photoperiod, and 65% relative humidity.

Larval development under natural conditions on *Schinus terebinthifolius* in Ilanot was from November 1, 1978 until March 31, 1979. On January 18, 1978 the W. Qilt population consisted of 2% eggs; 8% first instar larvae; 25% second instar; 41% third instar; 20% fourth instar; 4% fifth instar. The same population on March 16 consisted of only a few final instars and most were already in the ground. In the field the larvae feed together in a line or in mass as a group (Figs. 2 & 3) but do not form a tent as in some other species. In the final instar these masses of larvae are quite evident from a distance because of their dense white hairs (Fig. 3) Throughout the larval development, especially the final instar and the pupal cocoon, these hairs have an urticating effect upon contact causing an irritating allergic reacting as is known from other members of this genus.

Previous to pupation there is a period of wandering and prepupation lasting up to seven days. Pupation takes place several centimeters below the surface of the soil in a woven silk cocoon. Trought (1954) recorded the pupal period to be 7-8 months. We have recorded a pupation time of 6-8 months (adults Fig. 4) emerging from October 23 until December 14, 1978) in those reared under natural conditions of the Central Coastal Plain of Israel; however, some moths emerged in June-August 1979 after 14-16 months as pupae. No adults or new egg clusters were found during a June 27, 1979 survey of the W. Qilt site. Those reared at 27°C, 12 hour photoperiod, and 65% relative humidity emerged (after about 8 months) between September 30 and November 1; however, there was a high pupal mortality in this lab-reared population (83.3%). Larvae collected on January 18, 1978 in Wadi Qilt reared outdoors at Ilanot, entered the soil between March 17-27.

A tachinid fly *Palesia nudioculata* Villeneuve emerged on June 4, 1978 from a parasitized larvae (First host record for this fly).

From our observations of egg clusters and developing larval groups, the largest populations of *T. jordana* (as with its host) in Israel appear to be in Wadi Qilt and the surrounding area of the Judean Desert.

DISCUSSION

Biogeography

It is interesting to note that from a true biogeographical viewpoint, combined herbivore and host plant distribution, the host's

(Rhus tripartita) range is much broader than the herbivore's *(T.jordana)*. This is often the case even with host specific herbivores such as *T. jordana*. Only two of the other *Thaumetopoea* species are recorded as host species specific and one is the Irano-Turanian species, *T. cheela* Moore on *Rhus cotinus* in NW India (see Table 1). The range of *T. jordana* is restricted to a small part of its host's distribution and it does not evidently overlap with any other potential *Rhus* hosts, e.g. *R. coriaria* L. in northern Israel. *Rhus tripartita* is now relictual and was probably much more widespread in Pleistocene and Tertiary times, throughout the Saharo-Arabian regions. Because little fossil evidence exists, it is difficult to determine if *T.jordana*'s range was formerly broader. *T. jordana* is, like its host, a Saharo-Arabian element and this is also evident from the climate and ecosystem where it thrives in Israel and Jordan. It is apparently a restricted endemic in the Jordan Rift Valley with small peripheral or ocassional outlying populations becoming established (possibly only temporarily) in adjacent biotic provinces, i.e. Mediterranean garigue of Samaria.

It seems probable that the coevolution of *T. jordana* with its host has taken place to some degree since the host's range declined to its current relictual status. The species specificity of the Irano Turanian and Saharo-Arabian elements of *Thaumetopoea* to *Rhus* hosts may also indicate a rather advanced evolutionary step within this moth genus.

Coevolution of *Thaumetopoea*

Five of the ten species of *Thaumetopoea* feed on rather primitive plants, *Pinus* and/or *Cedrus*, and they may be the most primitive species or may have recently coevolved. However, they are probably similar in their phylogeny because all have biochemically coevolved with the secondary compounds in these two primitive plant genera. The most widely distributed species, *T. processionea*, feeds on *Oak* (widespread in the Mediterranean region) and could be considered either as an older autochthonous species or as a more recently evolved member of the genus.

The closest apparent relative to *T. jordana* (other than *cheela*) is *T. solitaria* with which it shares several interesting traits, including its host - *Pistacia* is in the same family (Anacardiaceae) as *Rhus*. This may suggest some similarity in the coevolution with secondary chemicals of the host plants. Also the larvae of *solitaria* are morphologically almost inseparable from *jordana*. These two Middle East Anacardiaceae feeders are evidently the only two (except the Baltic *pinivora*) that do not make larval tents. The major differences in their immature stages are phenological, e.g. pupation time.

B i o l o g y

It appears likely that there may be some chemical cue to ovipositing females of *T. jordana* from the new *R. tripartita* leaves because the first and only egg cluster recovered in the beginning of the 1978 flight season was found on a plant with the most (and the only significant) new foliage within a large area. Since oviposition takes place mostly in October, they are hatching during November and December; about the time of the early winter rains. Their development is thus correlated with the most abundant development of foliage and the winter precipitation in January.

Larval development takes place throughout the winter months and there are always larval masses at different stages of development. This seems to be advantageous because this type of staggering effect may prevent any one catastrophe from wiping out the entire population at once. Temperature has a distinct effect on larval development time which ranges from 40-70 days (at temperatures from 20°C to 30°C). In nature in the Judean Desert the mean winter temperatures are probably below 20°C and, therefore, a longer development time. It is also evident that relative humidity is important; an excess will retard the development time and may even cause some larval or pupal mortality. Temperature and humidity are, of course, very important factors in development of desert animals. It is interesting that *T. jordana* has a longer pupal development time (6-8 months) than the other five species of *Thaumetopoea* in the Middle East. This is presumably an adaptation (diapause) to the harsh conditions of the desert, during the dry season (April until October), that is comparable to over wintering in temperature climates. We confirm the presence of adults in May, reported by Amsel (1935) and Trought (1954), from reared adults that emerged from June to August after 14 to 16 months as pupae. We agree with Trought (1954) that this species is univoltine. This late emergence phenomenon is unusual and puzzling. *Thaumetopoea jordana* is apparently a more advanced member of its genus having evolved from the same lineage as *solitaria* but having adapted to a more xeric climate as a desert element (Saharo-Arabian) endemic to the Jordan Rift Valley of Jordan and Israel. It has specifically coevolved with its host, *Rhus tripartita*, presently a relict, previously more widespread across N. Africa and the Middle East.

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