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LIFE HISTORIES OF *TAENARIS* (NYMPHALIDAE) FROM PAPUA NEW GUINEA

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ABSTRACT. Descriptions and illustrations of the early stages and ecology of *Taenaris onolaus* Kirsch and *Taenaris catops* Westwood are given with a brief description and illustrations of the early stages of *Taenaris myops* Felder. Adults of both *T. onolaus* and *T. catops* were frequently seen imbibing cycad juices which probably enhances their assumed distastefulness to predators. Their foodplant specializations and aposematic attributes are discussed together with the mimetic relationships of *Taenaris*.

The genus *Taenaris* Hübner in Papua New Guinea numbers 18 species. Together with three species of the genus *Morphopsis* Oberthür and the monotypic genera *Hyantis* Hewitson and *Morphotenaris* Fruhstorfer, these are the only representatives of the Morphinae to be found in the country. A further six species of *Taenaris* and one of *Morphopsis* are known from Irian Jaya. Torres Strait marks the boundary of the distribution of these few closely related genera and species in the Melanesian region. They do not occur on the Australian mainland.

The Morphinae occur widely throughout the Indo-Australian region and number about 100 species. The morphology of the early stages and of the adults indicate their close affinity with the Satyrinae. For example, adults of *Morphopsis albertisi* Oberthür in Papua New Guinea superficially resemble the smaller satyrine *Tisiphone helena* Olliff. from north Queensland, Australia, where no mimicry could be involved.

Adults exhibit little sexual dimorphism, but males tend to be smaller than the females, have a more concave inner margin of the forewing and bear sub-basal androconial tufts on the hindwing.

Little was known of the biology of the Morphinae in the Melanesian region. Rosier (1940) gave some details of the biology of *Taenaris*

horsfieldii Swains. from Java and D'Abrera (1977) mentioned briefly the early stages and foodplants of *Taenaris catops* Westwood and *Taenaris phorcas* Westwood. D'Abrera stated that a paper describing the life history of *M. albertisi* was in preparation, but until now there has been no detailed study of any species of this subfamily published for the region.

Taenaris onolaus Kirsch

D'Abrera (1977) lists four races of this species, two occurring in Irian Jaya. The description of the subspecies *ida* Honrath fits the butterfly described here and this, therefore, represents an extension of its range from the known type localities for the subspecies in the Huon Peninsula. The 10 km grid square reference in which the subspecies has been found in Bulolo is DN50 at approximately 700 m. The present study was made from October to December 1979.

Egg (Fig. 2). 1.5 mm in diameter; pearly white when laid, changing within two days through cream to deep pink; almost spherical, but slightly tapered towards flattened apex; chorion covered with evenly spaced, shallow dimples. Duration, 14 days.

Larva. First instar. Length 4 mm on hatching, 5 mm at end of instar; head jet black, shiny with fine white setae; thorax and abdomen with fine white setae up to 1 mm in length, initially cream, gradually changing to yellowish green, then orange-red; prothorax with dorsolateral black spots. Duration, 2 days, and a further 5 days of inactivity during pre-ecdysis and ecdysis.

Second instar. Length 10 mm at end of instar; head jet black, shiny, 1 mm in diameter with setae 3.5 mm in length and pair of truncate, slightly forwardly curved horns 0.75 mm in length, each horn with 3 strong spines; thoracic setae 4 mm, abdomen with setae 3.5 mm in length; thorax and abdomen deep pink, abdomen with a dorsal black spot on anal segment. Duration, 4 days, plus 3 days of inactivity during pre-ecdysis and ecdysis.

Third instar. Length 22 mm at end of instar; similar to second but head 2 mm in diameter, horns 1 mm in length, each with 5 spines; thoracic setae 6 mm; thorax and abdomen pink with 4 indistinct, but continuous orange-yellow lines, 2 dorsolateral and 2 lateral. Duration, 6 days, plus 2 days of inactivity during pre-ecdysis and ecdysis.

Fourth instar. Length 35 mm at end of instar; head 3 mm in diameter, horns 1.5 mm, each with 6 spines; thorax and abdomen wine-red, orange-yellow lines slightly more prominent; body setae up to 9 mm in length; below these a layer of strong, sharp, black setae 1.55 mm in length. Duration, 5 days, plus 2 days of inactivity during pre-ecdysis and ecdysis.

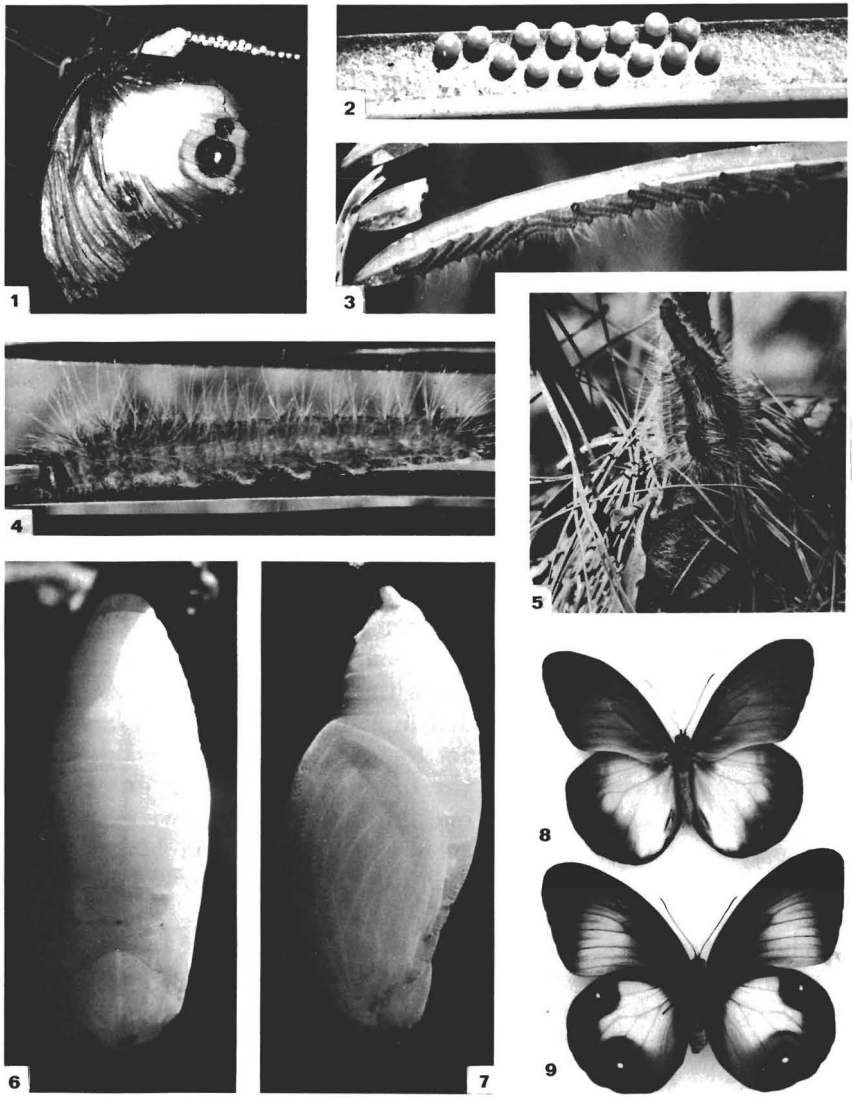
Fifth instar (Fig. 4). Length 60 mm at end of instar; similar to fourth but head 5 mm in diameter, horns 2.5 mm with 6 strong spines (Fig. 20c); body setae up to 10 mm; lower black setae 3 mm. Duration, 8 days, plus 2–3 days spent wandering.

Prepupa. Larval color changes from wine-red to yellow after suspension prior to pupation so that lower black setae and black spots of prothoracic and anal segments become very prominent. Duration, about 1 day of hanging before larva to pupa ecdysis.

Pupa (Figs. 6 & 7). Length 30 mm; ovate, smooth, translucent creamy white; cremaster black; anal rise with 2 black tubercles; apical margin of front bifid, forming 2 short, conical horns above each eye 1 mm in length. Duration, 17–20 days.

Ecological Observations

Foodplant and habitat. The foodplant is, unusually, a gymnosperm, *Cycas circinalis* (L.) Laut. & K. Sch. of the order Cycadales. This,



FIGS. 1–9. *Taenaris onolaus:* **1,** female ovipositing on cycad; **2,** eggs; **3,** second instar larvae; **4,** mature larva; **5,** mature larvae at rest in the leaf litter near the base of their foodplant; **6,** dorsal profile of the pupa; **7,** lateral profile of the pupa; **8,** upperside of male; **9,** underside of female.

however, is not a unique specialization among the butterflies. *Taenaris butleri* Oberthür is known from the same foodplant (T. Fenner, pers. comm.) and also *Luthrodes cleotas* Guérin of the Lycaenidae (Szent-Ivany et al., 1956). Another lycaenid, *Theclinesthes onycha* Hewitson, is also known from *Cycas* in Australia (Sibatani & Grund, 1978).

The foodplant exhibits a well defined distribution in the study area, being restricted to a well drained ridge alongside a gravel road behind the Bulolo Forestry College. The cycads cover about 3 acres which makes the area ideal for the study of a defined population of *T. onolaus*.

Cycas circinalis occurs locally at a quite high density (in places up to six plants per 10 square meters), mainly along the top of the ridge and under a 15 year old *Pinus* plantation. The plantation provides a fairly open habitat with only semi-shading by the thin pine canopy. Saplings of other trees occur sporadically throughout the plantation. These conditions appear to be ideal for the growth of the cycads and may explain why the plant is not found locally outside the area where the scrub becomes thicker. A number of plants were fruiting prolifically during visits to the area in October, November and December 1979, and there were many cycad nuts on the ground.

Oviposition and phenology. Eggs are laid by females in batches ranging in number from 20 to 40 with an average batch size of about 30. The highest number recorded in a single batch was 77. They are deposited close together, but not touching, on the undersides of one (or sometimes two) leaves of the older, tougher, dark green fronds. They are always placed about one third of the way down from the tip of the frond. Occasionally (seen in at least seven batches), there are one or two unfertilized eggs which remain white after the others have changed to pink.

The plants on which the females choose to oviposit are all of about the same height, approximately 1.5 m tall, and with usually 5–15 fronds. Cycads are extremely slow growing, and these plants are estimated to be from 5–6 years old (possibly older). As yet they have little or no trunk, and the fronds of most of them arise directly from the ground. No eggs or larvae were found on the younger plants with only two or three fronds and of smaller overall size at the beginning of the study period.

From observations of two females made late one afternoon in December from 1735 h onwards, it appears that *T. onolaus* only oviposits during the period of about two hours before complete darkness which is at 1900 h, dusk (or half-light) coming at about 1830 h. (This was suggested later by two further observations of females ovipositing at

dusk.) One female was discovered at 1745 h below a cycad frond, having laid about 30 eggs. Approximately every two minutes she deposited another egg in the row of four across the cycad leaf. Having completed a row she then moved slowly forward and positioned herself to begin a new row, from side to side. It is estimated, therefore, that a whole batch of about 50 eggs (this particular female had gone by the next morning but laid 45 eggs) would take approximately two hours to lay.

A second female was seen at the same time flying around another cycad, repeatedly settling on the upperside of a frond and then crawling beneath it. She then flew behind some vegetation, which obscured the other half of the same cycad, and settled out of sight. Soon after she was re-located sitting on a batch of about 25 newly laid eggs ready to recommence egg laying. It appears, therefore, that some females take periods of rest away from the cycads on which they are ovipositing then return to lay their eggs at intervals. Both females were still ovipositing in near darkness at 1850 h.

It is possible that females are able to lay further batches of eggs. However, it appears that their ovaries produce a certain number of eggs that are laid as a single batch in a short period of time. They are probably fairly short lived once they have paired and have finished ovipositing. It is also evident that females can detect the presence of eggs or larvae (probably visually) that are already present on the cycad, because when the area was studied in mid-November, no suitable looking plant was found to have more than one batch of eggs or larvae on it.

Eggs of *T. onolaus* were first discovered at the beginning of October 1979 which marked the end of an extremely dry dry-season. This lasted from the end of June for three months. During this time there was no rain recorded for the Bulolo Valley. In October, however, there were a few batches of *T. onolaus* larvae to be found, mainly fourth and fifth instars. Two egg batches were located at this time, which indicates that, even though the climate can be seasonally extremely dry in the area, generations can be continuous throughout the year because of the hardiness of the cycads; their foliage remains constant all the year round. (During the 1979 dry season in the Bulolo Valley, many angiosperms, especially vines, even in fairly dense forest areas, began to wilt and/or ceased new leaf growth. Often the dry season is hardly apparent.)

When the area was again revisited at the end of the first week in November, heavy rains had recommenced during the previous four weeks. At this time all but about eight suitable-looking plants had eggs

or larvae, and the approximate census was as follows: 18 batches of eggs, 7 groups of first instar larvae, 5 groups of second instar larvae and 2 of third instar larvae.

During the latter half of December females were still ovipositing, and a number of cycads, even the smaller, single-frond plants, were seen with newly laid egg batches. Some hosted up to three age classes of larvae, all of which fed together. This suggested that the area was now almost saturated with early stages due to the build up in numbers of adults and that intraspecific competition can occur where the species has limited, or finite, food resources. The few suitable cycads with no larvae at this time implied that any eggs laid on them may have been the subject of predation. Although no predators have been seen taking early stages, certain fresh egg batches were often found to have been eaten by the next day. Tetigoniid grasshoppers and predatory bugs are likely to be responsible.

In general, it may be concluded that as *T. onolaus* is a cycad feeder of tropical distribution, it is subject to little periodicity, i.e., that it is continuously brooded all year round, but that any large fluctuation in population numbers is reciprocal of extremes of wet and dry weather. Prolonged dry periods appear to produce aestivative (diapause) pupae and may also retard growth of new cycad fronds, so that the result at the onset of new rains is a large buildup of adults and early stages which compete intraspecifically for foodplants in areas with limited distribution of cycads.

Larval behavior. Larvae of *T. onolaus* are gregarious throughout their feeding period. In the fourth and fifth instars, however, the distance that separates each larva is increased, and they may be found feeding singly, or in sub-groups of up to five. First to third instar larvae spin an almost invisible mat of extremely fine silk on which they rest below the frond of the cycad, so that when the plant is viewed from above they are completely obscured from the observer.

When feeding, early instar larvae begin at the tips of the leaves of the cycad frond and eat each leaf back separately to the base of the main stem. The group will then begin to feed again on the next leaf and progress gradually downwards. They often defoliate a whole frond as they grow. The smaller larvae form very orderly rows when resting or as they feed on the edge of the leaf lamina (Fig. 3). Final instar larvae tend to be cannibalistic on soft, newly formed pupae if many are caged together. One particular batch of about 12 fourth instar larvae were found resting during the day at the base of a frond of one cycad and were thus hardly visible beneath the leaf litter trapped there (Fig. 5). This does not, however, appear to be typical behavior. They were not undergoing ecdysis, and it is possible that these larvae were

feeding at night and seeking shelter from predators during the day. All instars have been found feeding at various times during the day with no specific feeding or resting times.

In general, all instars are fairly slow in their movements. When touched they sometimes react by thrashing the head from side to side. This appears to be an effective means of warding off insect predators. Fifth instar larvae tend to curl up and fall off the cycad fronds if handled, behavior which enhances their very moth-like appearance.

Adult behavior and abundance. Females appeared to be most frequent in the study area and were seen at all times flying randomly throughout the pine plantation. Specimens were seen on every visit during the study period although never in great abundance at any one time. Numbers ranged on average from 1-4 (flying in close proximity) seen per hour.

At one time in mid-December a sample census resulted in the sightings during one hour of three males flying in a restricted gully on the border of the study area (one feeding on damp mud), and four females. Two of these females hung inertly beneath a cycad frond (late afternoon) and did not react to rapid hand movements nearby. One was picked up and promptly flew off when released. Invariably, however, adults are very wary and do not allow one to approach to within less than 2 meters if they are at rest and alert on the upperside of broad-leaved foliage.

There are no succulent fruit trees in the pine plantation, and none of the saplings which produce small berries that fall to the ground have proven attractive to adults. However, on a number of occasions both sexes have been seen feeding on the fermenting skins of cycad nuts that have fallen to the ground when brown and ripe.

Competition. Intraspecific competition has been mentioned. However, there also exists in the area, interspecific competition for *Cycas circinalis* between *T. onolaus* and a chrysomelid beetle of the subfamily Criocerinae. The small 1 cm long, orange beetle which is probably *Crioceris clarkii* B. Baly (based on the discussion in Szent-Ivany et al., 1956), feeds as a cream colored larva on the cycads. It has a definite preference for the soft, new, light-green cycad fronds. Therefore, by selecting only the older tougher fronds on which to oviposit, *T. onolaus* probably avoids competition for individual plants. Nevertheless, the beetle does cause much damage to the cycads in the area and can be classed as a successful competitor with *T. onolaus*.

The feeding damage caused by the beetle larvae is very characteristic. Even for a long time after a cycad has been eaten back by either herbivore it is possible to determine whether it was fed on by beetle or butterfly. Whereas *T. onolaus* eats the whole leaf of a frond, the

chrysomelid eats only the underside of a lamina and leaves the top waxy cuticle as a window. This soon dries, turns yellow, and is left trailing, still attached to the frond.

Many new, recently unfurled, cycad fronds were the subject of attack by the beetle in mid-December 1979. These beetles also appear to play a significant rôle in controlling the population size of the butterfly. It is possible that they cause a final crash in the numbers of a cohort of *T. onolaus* because, if there are sufficient numbers of the beetle, then growth of cycads in the area may be halted completely. There will not, therefore, be enough fronds which reach maturity for the benefit of *T. onolaus.*

Taenaris catops Westwood

D'Abrera (1977) lists 21 races of this species. As emphasized by Brooks (1950) the named subspecies of *T. catops* may be very artificial as the species is widely distributed in New Guinea, of common status, and exhibits a great phenotypic variability both locally and regionally. Considering for example the supposed subspecies *mylaecha* from Sudest Island which is described by D'Abrera as an "albinotic extreme" (i.e., very white), the same form is now recorded widely from the Western Highlands Province of the mainland (Fig. 22). The other extreme is an extremely dark form of *T. catops,* in which black and dark grey have replaced almost all the white. Supposed subspecies of *T. catops* should, therefore, be accepted with caution and are more likely the result of clinal variation or Müllerian mimetic associations within their genus.

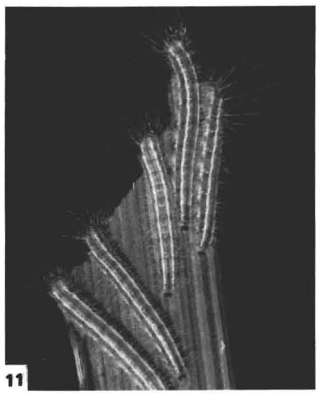
The life history of this species was also recorded from the *T. onolaus* study area in March and April 1980. The egg and first two instars cannot be described as only the third instar onwards were available.

Third instar (Figs. 10 & 11). Larvae grew extremely rapidly from 8 to 25 mm in 3 days; head jet black, shiny, 2 mm in diameter, covered with fine white setae, horns similar to those of *T. onolaus,* 1.5 mm in length; body covered with soft, white setae, longest (5 mm) on the prothoracic and anal abdominal segments, decreasing to 4 mm at body center; thorax and abdomen dark grey with 2 dorsolateral and 2 lateral white lines; spiracles encircled with yellowish orange; claspers laterally yellowish orange, dorsally with black patch surmounted by two short (0.55 mm) pointed tubercles. Duration, 3 days, plus a day of inactivity spent during pre-ecdysis and ecdysis.

Fourth instar. Length 32 mm at end of instar; similar to third but body laterally black with middorsal black line bordered with grey. Duration, 7 days, plus 1½ days of inactivity spent during pre-ecdysis and ecdysis.

Fifth instar (Fig. 12). Length at end of instar 57 mm; similar to fourth but head 4.5 mm in diameter, horns with 8 long, thin spines (Fig. 20a); body jet black but for 2 dorsolateral white lines and 2 lateral yellow lines; spiracles black encircled with orange; soft white setae 7 mm longest; strong, sharp lower setae tan brown, 2.5 mm in length. Duration, 9 days.

Pupa (Figs. 13 & 14). Length 31 mm; smooth ovate, pale green; cremaster pale yellow,



FIGS. 10–15. *Taenaris catops:* **10,** third instar larvae at rest; **11,** third instar larvae feeding; **12,** mature larva; **13,** ventral profile of pupa; **14,** lateral profile of pupa; **15,** adult female imbibing the juices of a damaged cycad nut.

tipped with black. In shape pupa like that of *T. onolaus* but frontal horns slightly longer, more pointed, tipped with yellow and below this is a ring of pale brown; tubercles of anal rise not as prominent as those of *T. onolaus*, only faintly tipped with brown. Duration, 12 days.

Ecological Observations

Foodplant and habitat. The early stages of *T. catops* were discovered at the center of the *T. onolaus* study area previously described. The foodplant is a new record for *T. catops*. It is a 1.5 m tall ground orchid with large, predominantly white flowers, *Phaius tancarvilleae* (Banks in L'Herit) Bl. The plant has been found in the Bulolo Valley at 800 m growing under *Pinus* in the plantation. This may not, however, be the usual foodplant for the species as D'Abrera (1977) states that *T. catops* feeds on the Black Palm (*Caryota rumpha:* Palmae), Betel-nut palm (*Areca catechu:* Palmae) and Banana (*Musa:* Musaceae). Pyle and Hughes (1978) list *T. catops* from *Cordyline terminalis* (Liliaceae) which is used in hedges in many highland areas of the mainland.

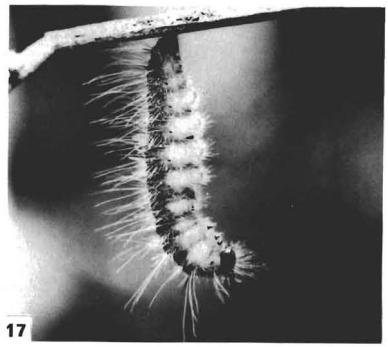
Larval behavior. Like *T. onolaus*, the larvae are gregarious and remain so up to the final instar. They feed in line from the tip of the leaf lamina and eat the blade gradually downwards to halfway or a little less (Fig. 11). The larvae pause at intervals and then move slightly back up the blade to rest.

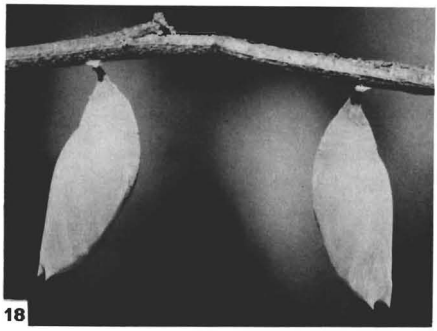
Adult behavior and abundance. Females of *T. catops*, like those of *T. onolaus*, were more often encountered in the area than males. They were also slightly more abundant than those of *T. onolaus*. Occasionally, up to five at one time were seen in one area.

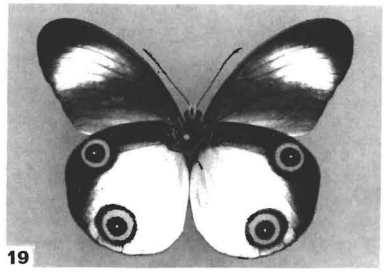
T. catops has also been found just before dusk hanging inertly beneath foliage. Only at this time can they be approached because they are otherwise always alert and wary when feeding or resting on the uppersides of leaves. In forest areas they prefer to fly in shade. The species has been observed in many localities on the mainland flying just above the leaf litter in search of fermenting fruits on which to feed or probing moist leaf litter.

In spite of their preference for shady habitats, both sexes of *T. catops* can commonly be seen flying through gardens in Bulolo and in straight lines across any open grassland areas in the Bulolo Valley. In sharp contrast, *T. onolaus* has never been observed outside the study area.

It is interesting to note that both *T. catops* and *T. onolaus* were fond of visiting the fermenting husks of cycad nuts on the ground (Fig. 15). At one time a female of *T. onolaus* was seen feeding between two *T. catops* females. At another time five *T. catops* were flushed from beneath two close-growing cycads on which the chrysomelid beetle larvae were feeding. They were seen to probe the fresh green frass of the beetle larvae where it had fallen to the ground. On numerous occasions the cut ends of cycad fronds on the ground which had exuded sap were seen to be extremely attractive to *T. catops*—this is discussed further below.







FIGS. 16–19. *Taenaris myops:* **16,** mature larva; **17,** prepupal larva; **18,** latero-ventral profile of pupae; **19,** underside of male.

Taenaris myops Felder

D'Abrera (1977) lists 13 races of this species. Its full life history was studied from a batch of 37 eggs. These were collected from the underside of the leaf of a monocotyledon, *Tapenochilus* sp., of the Costaceae found in November 1980, growing on a creekside near Eilogo Falls (Port Moresby, Central Province, 10 km grid square EK45). This represents a new foodplant record. However, as the author, after locating the eggs and watching them hatch, had other commitments, the early stages of *T. myops* were reared and photographed by Peter Clark. He noted that, in general, the whole life history was similar to that of *T. catops*.

Egg. Slightly lighter pink but otherwise similar to that of *T. onolaus*.

Larva. First instar. 4 mm long on hatching; head jet black, shiny, covered with fine white setae; body with long fine white setae, up to 1 mm in length; thorax and abdomen opaque creamy white, gut from behind head to last 4 abdominal segments shows as pinkish red line, anal segments with traces of pinkish red.

Second to fourth instars. Larvae at each instar exhibited similar growth rates and maximum sizes as those of *T. catops*. They grew steadily darker so that by fourth instar they were brownish black.

Fifth instar. Length 59 mm at end of instar; head horns with 6 spines (Fig. 20b);

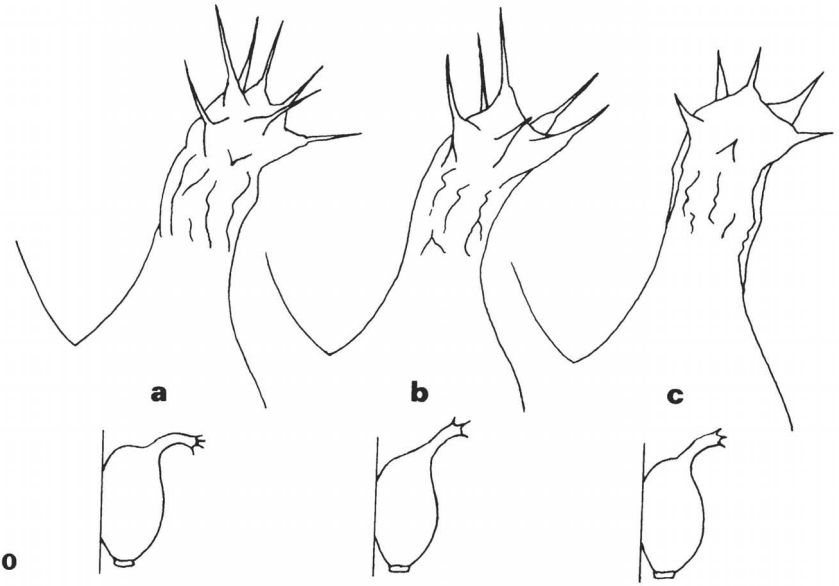


FIG. 20. Frontal profile of left horn and lateral profiles of *Taenaris* final instar larval head capsules: **a**, *T. catops*; **b**, *T. myops*; **c**, *T. onolaus*.

prothoracic segment wine-red, remainder of thorax and abdomen jet black, not lined as larvae of *T. onolaus* and *T. catops*; spiracles black, encircled with wine-red; body setae soft, long, white, laterally 4 mm, dorsally 10 mm in length; lower strong, black setae 4 mm longest.

Prepupa (Fig. 17). Larval color changed to dark grey dorsally and pale green ventrally after larvae had suspended themselves prior to pupation. Pupation took place 40–42 days after larvae hatched.

Pupa (Fig. 18). 30 mm in length; shape like that of *T. onolaus* but color like that of *T. catops*. Duration, 13 days.

The overall duration from the time that the eggs hatched to the emergence of the adults was 54 days. *T. myops* has been previously recorded in Papua New Guinea feeding on coconut (*Cocos nucifera*) and oil palm (*Elaeis guineensis*) both of the Palmae (Dept. Primary Industry, unpublished).

DISCUSSION

Cycads are known to be toxic and often lethal to cattle. Whiting (1963) discussed the toxicity of cycads in general, and Yang and Mickelsen (1968) have shown that the husk of *Cycas circinalis* is toxic to rats. It is quite probable, therefore, that the larvae of *T. onolaus*, like many "pharmacophagous" butterflies (the *Aristolochia*-feeding swallowtails, for example), can sequester, and store, certain compounds (such as bitter alkaloids) which render them distasteful to birds and other predators. Their bright wine-red color suggests this. The larvae

of *T. butleri,* which also feeds on cycads, are also wine-red (T. Fenner, pers. comm.).

It is possible that the larvae of *T. catops* and *T. myops* are more palatable to their predators, because their foodplants are not known to have toxic properties. Other species and their foodplants, which have not yet been mentioned but which are relevant to this discussion, include *Taenaris artemis* Vollenhoven on coconut (*Cocos nucifera:* Palmae) and *T. phorcas* on tanget (*Cordyline:* Liliaceae) (T. Fenner, pers. comm.). Rosier (1960) has found the wine-red larvae of *T. horsfieldii* on *Smilax* (Smilacaceae) and, according to Corbet and Pendlebury (1978), the closely related genus *Faunis* in Malaysia feeds on *Smilax* (Smilacaceae), *Musa* (Musaceae) and *Pandanus* (Pandanaceae). Recent records of other *Taenaris* foodplants sent into the Insect Farming and Trading Agency include *Taenaris dimona* Hewitson on banana (*Musa:* Musaceae) and *Taenaris gorgo* Kirsch on Black Palm (*Caryota rumpha:* Palmae). Both records were from the Maprik area, East Sepik Province. I have recorded the life history of *Taenaris artemis* on *Pandanus* (Pandanaceae) in the Western Province. The larvae were predominantly yellow marked with black.

Although *Taenaris* larvae do not appear to advertise their presence, all species nevertheless feed gregariously, which is behavior characteristic of distasteful Lepidoptera. However, on some foodplants the larvae of certain *Taenaris* species may be unable to store adequate secondary plant compounds for their effective protection. If *T. catops* obtains no such protection by feeding on ground orchids, then this may explain why adults were seen to imbibe cycad juices and consequently were so common in the study area. A similar conclusion was reached by Edgar et al. (1976) for danaine butterflies that enhanced their unpalatability by visiting the withered leaves of plants which produced pyrrolizidine alkaloids. The observation that *T. onolaus,* even as an adult, imbibed cycad juices strongly supports the hypothesis that *Taenaris* is a distasteful group of butterflies and that some species enhance this as adults. It may be added that the fermenting skins of cycad nuts have an extremely nauseating smell.

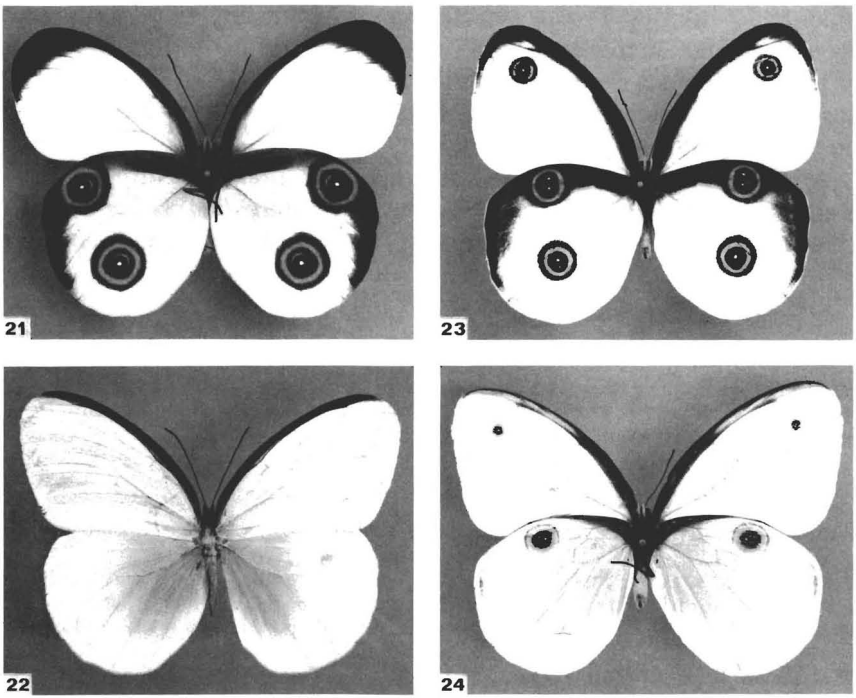
All species of *Taenaris* so far studied in the field have exhibited great wariness and are quick to avoid capture. This, together with their eyespots and the protective hairs and bristles of their larvae, may be considered to be secondary lines of defence if they have been retained from an ancestral form that was more cryptically colored and in which these characters were of primary protective function. Such an ancestor may have looked like the small, dull, species of *Faunis* found in Malaysia today. The general trend to enhance the aposematic attributes

of *Taenaris* appears to have been for the butterflies to increase in size, to become lighter, and for the eyespots to become enlarged and highlighted with broader orange borders. Of the cycad feeding species so far studied, the ground color is predominantly black, and the extent of the orange has been greatly increased so that it is highlighted as a warning color. It is interesting to note that the same also appears to be true of the cycad feeding lycaenid *Luthrodes cleotas* from Papua New Guinea which has large patches of orange on the upper and underside of its hindwings in both sexes.

It is possible that the ability of certain *Taenaris* species to feed on cycads as larvae is a recent evolutionary advance. J. Holloway (pers. comm. in discussion) suggested that the initial transfer to these primitive gymnosperms may have been a result of the similarity in the appearance of cycad fronds and those of coconut palms, for example, so that some *Taenaris* females began to oviposit on them by mistake. Alternatively, the transition from angiosperms, such as palms, to the cycad gymnosperms may have been through other angiosperms (such as *Cordyline* or *Tapenochilus*), that acted as "bridges," i.e., they contained secondary substances that were common (or similar) to both. These may have acted either as oviposition cues to the females or phagostimulants to the larvae. The fact that adults of *T. catops* imbibe cycad juices could be taken to imply a closer link of this species with cycads in the past; however, it is also indicative of a chemical similarity between its normal foodplants and cycads.

T. catops exhibits a wide range of geographical forms and it is probable that it is a Müllerian mimic of its close relatives. A recent sampling of *Taenaris* in the Cape Rodney area, Central Province, revealed what appears to be a Müllerian mimicry complex involving four species of morphines (pers. obs., Dec. 1979). These were *Hyantis hodeva* Hewitson, *Taenaris mailua* Grose-Smith, *T. catops* and *T. myops*. They were all extremely alike, and in particular, *T. catops* was more heavily marked than usual with extended black margins to the apices of the fore and hind wings. *T. mailua* differed in the area from the form of the nominate race and was slightly less heavily marked with black. It appears, therefore, that there was a convergence of the phenotypes of all the species in the area. All four species looked identical on the wing.

Müllerian mimicry within the Morphinae appears to be a widespread phenomenon throughout New Guinea in general, and another good example has been recorded from Minj in the Western Highlands Province between *H. hodeva* and *T. catops* where the extremely white form of *T. catops* is predominant (Figs. 22 & 24). *H. hodeva* in the area is almost white, lacks its usual heavy black apical margins and has



FIGS. 21–24. Müllerian mimicry in female morphines: **21,** normal *Taenaris catops* from Bulolo; **22,** albinotic *T. catops* from Minj; **23,** normal *Hyantis hodeva* from Bulolo; **24,** albinotic *H. hodeva* from Minj. (Males from the two localities are like their females.)

reduced eyespots. In and around the Bulolo Valley the same species are also alike, but in this locality they are heavily marked (Figs. 21 & 23) and conform to the more normal and widespread phenotypes.

Other butterflies are probably Batesian mimics of *Taenaris*. For example, the female of *Mycalesis drusillodes* Oberthür is thought to be mimetic of *H. hodeva* (Vane-Wright, 1971). Both model and mimic have been collected from the Torricelli Mountains near Maprik in the East Sepik Province (P. Clark, pers. comm.) and at Mt. Bosavi in the Southern Highlands Province (pers. obs., April 1980). The satyrine genus *Elymnias* is apparently mimetic of certain species of *Euploea* (Danainae), and *Elymnias agondas* Boisduval females are extremely good mimics of *Taenaris bioculatus* Guérin and *T. catops* where the models and mimics occur sympatrically. *Hypolimnas deois* Hewitson (Nymphalidae), in color and pattern, is very *Taenaris*-like and may be mimetic of *T. onolaus* in the Bulolo Valley. It is also assumed that the female form *onesimus* Hewitson of *Papilio aegeus* Donovan (Pa-

pilionidae) mimics *T. catops*, and this form is also commonly seen around Bulolo. If this is so, then the female form *amanga* Boisduval of this swallowtail is a good candidate to be a mimic of *T. onolaus*. It has been seen frequently in the study area and strongly resembles *T. onolaus* in flight.

A more detailed study of the foodplant relations and mimetic associations of these butterflies will prove most interesting as further life-histories and the foodplants of other species of *Taenaris* are discovered.

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