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MIGRATION AND OVERWINTERING AGGREGATIONS OF NINE DANAINE BUTTERFLY SPECIES IN TAIWAN (NYMPHALIDAE)

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ABSTRACT. Nine species of danaine butterflies regularly participate in fall migrations of 300 km or more from the temperate northern and montane areas of Taiwan to several warmer sheltered valleys in the southern part of that island. There they aggregate by November and December in overwintering colonies at 300–500 m above sea level. *Salatura genutia* generally forms single-species colonies of up to 50,000 butterflies. The other eight species form mixed-species colonies of thousands of individuals. The winter temperatures in the colony sites normally remain above 10°C. In late March, the overwintered danaines begin courting and mating, and then individually fly north to the breeding areas.

Additional key words: *Euploea, Parantica, Radena, Tirumala, Salatura.*

Apparently in response to the strongly seasonal climate on the northern half of Taiwan, an extraordinary intra-island migration and subsequent formation of a series of overwintering aggregations takes place annually among at least 9 of the 18 species of Danainae (Nymphalidae) among the 400 species of butterflies living on this Asian island. These danaine butterflies fly southward in groups before the onset of winter, and congregate in several warm and windless valleys located in the southern part of Taiwan where they pass the winter. Local people have long known of the existence of these overwintering valleys, calling them "Butterfly Valley" or "Purple Butterfly Valley," but only recently have scientists investigated these phenomena. Here we summarize the known information about these extraordinary migrations and overwintering aggregations.

Taiwan Geography and the Locations of Overwintering Sites

The Southeast Asian island of Taiwan covers some 36,000 square km and is approximately 394 km in length from north to south. A plains area occupies the western third of Taiwan while the remainder of the island is covered by the Central Mountain Range, which runs some 320 kilometers from north to south. The main Taiwanese peak of Yushan

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rises 3997 m above sea level and is the highest mountain in Southeast Asia. More than 130 mountain peaks on Taiwan reach higher than 3000 m elevation. As elevation increases, even in the areas of Taiwan south of the Tropic of Cancer, temperature decreases correspondingly; above 2500 m elevation, winter snows occur.

The first overwintering aggregation of butterflies was discovered by an unknown Taiwanese lepidopterist in 1971. Today, four locations have been found where large overwintering aggregations of these danaines occur regularly. All of the butterfly valleys are located in the low mountains of Kaoshung County, Pinton County, and Taiton County, three of the southernmost counties of Taiwan (Fig. 1). From north to south, these sites are: Lukuea, Taiwu, Laiyi (all on the western side of the Central Mountain Range), and the most recently discovered overwintering site, Dawu, found by Wang during the winter of 1988–89 and located 46 km S of Chipen Hotspring in Taiton County, on the eastern slope of the Central Mountain Range.

The three sites on the western side of the Central Mountain Range are occupied primarily by overwintering species of the genus *Euploea*, whereas at the single eastern slope site, half of the danaines in the overwintering colony are species of *Radena*, *Tirumala*, and *Parantica*. The most abundant species is *Radena similis similis*. A preliminary hypothesis (Wang unpublished) relates this interesting distributional difference to the distribution of the food plants of these genera. Initially, the butterflies occupy sites with altitudes in excess of 1000 m, but, as winter progresses, the butteflies move downslope to the final overwintering sites at elevations between 300 and 500 m.

Species Involved in the Overwintering Aggregations

The overwintering species of danaine butterflies in Taiwan include the following (larval food plant observations by Wang):

1. *Euploea sylvester swinhoei* (Wallace) (Plate 1: k)

   The larval food plants are species of *Ficus* (Moraceae). Widely distributed in Asia, this species occurs from Sri Lanka and southern India to southern China and south through Indonesia and Malaysia to New Guinea, as well as the Philippines and northern Australia. Elsewhere, individuals of *E. sylvester* have been observed migrating through the Port Moresby area in Papua New Guinea (Ackery & Vane-Wright 1984).

2. *E. eunice hobsoni* Butler (Plate 1: l, m)

   Three species of the fig family are the larval food plants: *Ficus microcarpa*, *F. ampelos*, and *F. formosana*. The butterfly and its

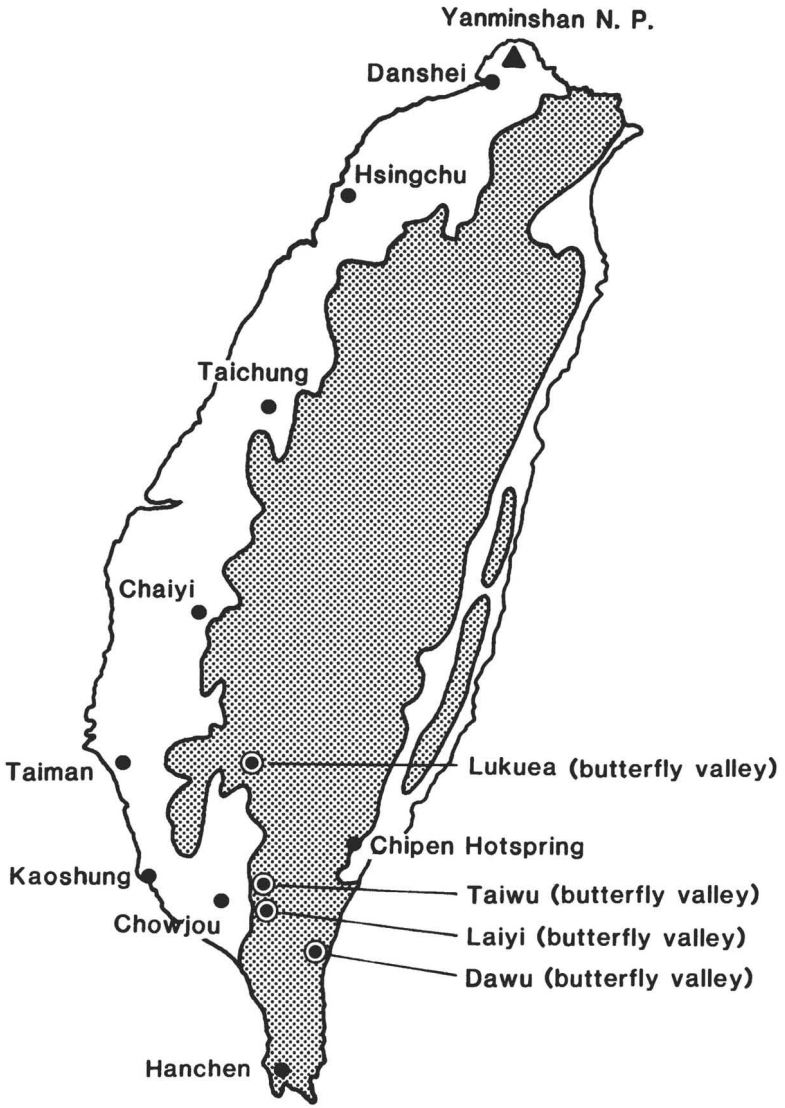

FIG. 1. A map showing the mountain areas (shaded) of Taiwan, and the locations of the known overwintering valleys and major landmarks.

food plants are distributed in all montane areas of the island, from the lowlands to 1500 m. Elsewhere, the species occurs from the southern coast of China through Indo-China and the Philippines. Williams (1930) reported *eunice* as a migrant in December 1885 in Java (under the name *leucostictos*).

3. *E. mulciber barsine* (Fruhstorfer) (Plate 1: f, o, p)

Six species of *Ficus* are larval food plants in Taiwan: *Ficus microcarpa, F. pumila, F. sarmentosa, F. vasculosa, F. erecta,* and *F. formosana.* The butterfly ranges from lowland elevations to 2000 m in all mountain areas of Taiwan. On mainland Asia, *E. mulciber* is widespread from India to the Philippines and southern China. Williams (1930) notes several records of this species migrating in vast numbers with other butterflies in Burma (January) and Thailand (May).

4. *E. tulliolus koxinga* (Fruhstorfer) (Plate 1: n, q)

This species feeds on unidentified *Ficus* in Taiwan; elsewhere, it uses *Malaisia* species (Moraceae) and *Nerium oelander* (Apocynaceae) (Ackery & Vane-Wright 1984). It is widespread across Asia and the South Pacific islands to Australia; there is one report of a large-scale migration of *E. tulliolus* in Malaysia (Batchelor 1960).

5. *Parantica aglea maghaba* (Fruhstorfer)

Two species of Asclepiadaceae serve as larval food plants: *Tylophora lanyuensis* and *T. ovata.* The butterfly is distributed from the lowlands to 1000 m in all the mountains of the island. Widespread across Asia from India and Sri Lanka to China, this species has been reported to occur occasionally in small numbers in migratory flocks of other butterflies in February, August, and October in south India and Sri Lanka (Williams 1930).

6. *Ideopsis (Radena) similis similis* (Linnaeus) (Plate 1: e)

The food plants of *I. s. similis* are *Tylophora ovata, Cynanchum atratum,* and *Marsdenia tinctoria,* all in the family Asclepiadaceae. The butterfly occurs in all mountain regions from the lowlands to 2500 m. There is one record (Williams 1930) of this species migrating in a mixed species flock on 23 May 1926, in Thailand, moving southward in the morning by the millions and to the north the same afternoon in low numbers.

7. *Tirumala limniace limniace* Cramer

The larval food plants are *Dregea formosana* (Moraceae) and *Heterostemma brownii* (Asclepiadaceae). The butterfly ranges from the lowlands to 1500 m in all mountain areas of the island. On the Asian mainland, this species is widespread from India to China, the Phil-

ippines, and south through the Indonesian islands. Williams (1930) records a number of southern migrations of *T. limniace* on the island of Sri Lanka from late September to early December, and cites a 1912 report that "it migrates annually from the plains in the district of Kodaikanal, S. India, in October and November with many other species" (Williams 1930:159).

8. *T. hamata septentrionis* (Butler) (Plate 1: i)

The larval food plant is *Heterostemma brownii* (Asclepiadaceae). The butterfly is distributed in all montane areas of Taiwan, from the lowlands to 2000 m. It is primarily a mainland Indo-Oriental species, with relatively few island populations in Asia. Williams (1930) cites a number of reports of *hamata* migrating in low numbers in mixed-species flocks in October, January, and March in India, Sri Lanka, and Burma. In southern India, it is reported (Williams 1930) to move annually from the plains in October and November.

9. *Danaus (Salatura) genutia genutia* (Cramer) (Plate 1: j)

Danaus genutia feeds on three species of Asclepiadaceae: *Asclepias curassavica, Cynanchun lanhsuense,* and *C. taiwanianum.* It flies from the lowlands to 1000 m in all island mountains. Elsewhere, *D. genutia* flies from China and the Philippines through Indonesia to northwestern Australia (but not in New Guinea) and west to India (Ackery & Vane-Wright 1984). There are no previous reports of migratory behavior in this species. However, Longstaff (1912:756) observed a group of about 20 *Danaus genutia* gathering to roost communally under a palm leaf in the evening on 8 December 1903, in the Botanic Gardens at Howrah near Calcutta, India.

The relative proportions of eight of these species found at the Lukuea overwintering site in Kaoshung County in mid-winter 1989 are shown in Table 1. Here, at 400 m elevation, the quiescent adults were sitting on the upper surfaces of leaves and twigs on a variety of tree species. Most resting butterflies were between 3 and 10 m above the ground.

Most (86%) of the overwintering danaine butterflies in this sample (counted by H. Y. Wang) belonged to the genus *Euploea.* The two most common were *Euploea mulciber barisine* and *E. tulliolus koxinga.* All four species of *Euploea* are widespread over the island of Taiwan, but can be collected only from April to September in the northern and central part of Taiwan. In other words, these four species of *Euploea,* along with the other migratory danaine species, "disappear" from the northern and central areas of Taiwan from October to March of the

TABLE 1. The proportions of individuals among eight species of danaines in an overwintering site sample (206 specimens) counted 17 February 1989 by H. Y. Wang, at Lukuea, Kaoshung County, Taiwan (400 m).

Species	Number	Percentage of aggregation
1. *Euploea tulliolus koxinga*	76	36.9%
2. *E. mulciber barsine*	68	33.0%
3. *E. eunice hobsoni*	22	10.7%
4. *E. sylvestor swinhoei*	12	5.8%
5. *Tirumala hamata septentrionis*	12	5.8%
6. *Ideopsis similis similis*	10	4.9%
7. *Parantica algea maghaba*	1	0.5%
8. *Danaus genutia genutia*	5	2.4%
Total	206	100.0%

following spring, apparently concentrating in these several southern valleys for the winter (Table 2). Incidentally, all of these species formerly were placed in the "catch-all" genus *Danaus*, congeneric with the well-known migrant North American monarch butterfly, *Danaus plexippus*.

Danaus genutia, although rare in the mixed aggregations (Table 1), forms large single-species overwintering colonies, as does the monarch in Mexico. Unlike the huge aggregations of monarchs in Mexico, however, which number in the millions, colonies of *D. genutia* number in the hundreds or thousands, and have never been found to exceed 50,000 individuals. This species has a beautiful orange and black color pattern on the dorsal wing surface, similar to the monarch.

In contrast to *D. genutia*, *Ideopsis similis similis*, a beautiful pale green butterfly with black veins, overwinters in low numbers in the same valleys as other danaine species.

In the summer season, a time of maximum flight activity, individuals of local populations of *I. similis* congregate in small groups in late afternoon, sitting on adjacent leaves to pass the night.

Characteristics of the Migratory Behavior

Although the first butterfly valley in Taiwan was not reported by a lepidopterist until 1971, considerable local interest has focused on the phenomenon since. One central fact already known is that before the first major cold front sweeps across Taiwan, usually in late November, all the overwintering species of danaines have reached the butterfly valleys or nearby areas (Wang, pers. obs.). A general outline of other behavioral observations to date is as follows.

Initially, danaines at the same elevations in the higher mountains form small mixed-species groups that fly south along the Central Moun-

TABLE 2. Seasonal occurrence of migratory and non-migratory danaine butterfly species at Yanminshan National Park, located at the most northern point on Taiwan (Fig. 1). (The symbol "+" indicates the resident occurrence of the species in that season.)

Species	Spring	Summer	Autumn	Winter	Migratory in Taiwan or not
Euploea sylvestor swinhoei	+	+			yes
E. mulciber barsine	+	+	+		yes
E. tulliolus koxinga	+	+	+		yes
E. eunice hobsoni	+	+	+		yes
Tirumala hamata septentrionis	+	+			yes
T. limniace limniace	+	+			yes
Ideopsis similis similis	+	+			yes
Parantica aglea maghaba	+	+			yes
P. malaneus swinhoei	+	+	+	+	no
P. sita niphonica	+	+	+	+	no
Danaus genutia genutia	+	+			yes
Limnas chrysippus	+	+		+	no

tain Range. Other small groups form and join together to increase the size of the migrating aggregations. As the large migratory groups reach the southern area of the Central Mountain Range, they settle temporarily in valleys in the higher mountains, at altitudes in excess of 1000 m. When an arriving cold front from mainland Asia (Fig. 2) lowers the air temperature, the large group flies downslope into the warmer valleys. In the process, larger and larger groups of butterflies form as smaller groups encounter each other. The result is like a snowball rolling downhill, with the migrating group growing steadily on the way to its winter home. This portion of the migration, forced by the arrival of cold fronts from the Asian continent, presents spectacular scenes, but it is difficult to observe movements of these large aggregations for the following reasons:

(1) The *migratory distances* involved in the last stages of the migration route are short.
(2) The *migratory time* required for these relatively local movements from high mountains to lower valleys is brief, taking place in only a day or so.
(3) Most of the species in these groups are black and purplish or green, and are well *camouflaged* within the forest. Additionally, they fly only a meter or two above ground and thus are frequently inconspicuous within the thick tropical vegetation at the southern end of the island.

The number of times that this kind of local migration is repeated during a single year depends on how many strong cold fronts arrive

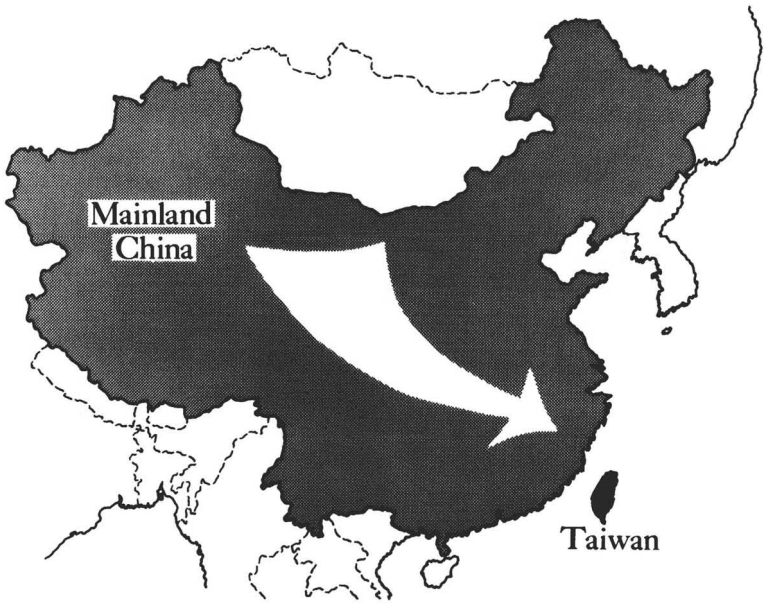

FIG. 2. The geographic position of Taiwan and the direction of cold fronts arriving from mainland Asia in winter.

during the late fall and winter. Finally, however, the huge group of danaines finishes migration and arrives at the lowest and warmest valleys, where it stays until the coming of spring. Usually, these last sites in the overwintering valleys range from 300 to 500 meters in elevation. After their arrival at these locations, no matter how cold the weather is, the danaines never have been observed to move to other places or to leave the mountain valleys to enter the lower but developed (urbanized and agriculturalized) plains areas.

If an extraordinarily strong cold front arrives and causes the temperature in these final overwintering valley locations to drop below 4°C, disastrous losses occur in the colonies. Frozen danaids cannot hold their positions on the leaves and fall to the ground in quick succession. The forest floor becomes carpeted with dead butterflies, coloring the ground with masses of black, purple, and green wings and bodies. Normally, however, the temperature in the southern low mountain areas very seldom drops below 4°C.

The southward and downard movement of danaines that normally live in high mountains results in their arrival at these southern warmer valleys where past generations have survived the winter. At higher elevations, nighttime temperatures regularly drop below 4°C during

the winter. However, the lowest temperatures in the now-cleared and uninhabitable plains areas during the winter are above this level. For example, between December 1988 and February 1989, the lowest temperatures anywhere in the plains occurred at dawn on 12 February 1989. Minimum temperatures on the plains, which occur in February, are lowest in the North and increase gradually from north to south as follows (refer to Fig. 1): 6.4°C (Danshei), 7.2°C (Hsingchu), 6.9°C (Taichung), 7.2°C (Chaiyi), 8.5°C (Taiman), 10.2°C (Kaoshung), and 10.7°C (Hanchen). This temperature gradient suggests an ecological reason for the southward movement and the selection of lower-elevation sites by populations of overwintering danaines, where they seek winter shelter on trees still existing in foothill valleys just above the developed plains area.

Some of these migrations reach spectacular numbers. A local lepidopterist named Chan reported to Wang that he saw "a flying black river" of danaine butterflies flowing from the sea to the nearby valley at Chow-Jou Beach (in Pinton County) in early December 1972. Chan hypothesized that the danaines living in the lowlands or the western plains fly from the breeding area directly to the coast, and then fly southward above the Taiwan Strait and the adjacent coastline, gradually joining with other groups. The migrating danaines then become a very large group when they approach the turning point at the Sea of Chow-Jou. At that point, the danaines form a huge and lengthy flying river from sea to the land as they fly inland towards the overwintering valleys. This use of a coastal route by migrating danaines may result from the fact that the entire western plain of Taiwan is now developed. Urbanization and industrialization of these western lowlands have eliminated any past favorable nectaring areas or other natural habitats and navigational landmarks that might have been used by the danaines.

Behavior in the Aggregation Valleys

In the latter part of November and December, danaines that have just arrived at the overwintering valleys take up positions on the leaves, but fly around actively from approximately 0930 to 1130 h (Plate 1). They also visit nearby streams for drinking water during the same period. However, when cold fronts come, the butterflies remain motionless on tree leaves in the valley until warmer temperatures return.

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PLATE 1. Scenes of the overwintering phenomenon in Taiwanese danaine species. (a) Overwintering danaine aggregations take flight on warm days or when disturbed by people entering a colony area. (b) Hundreds of dark *Euploea* individuals rest in scattered array on the top surfaces of leaves of deciduous trees while overwintering. They are not

as densely packed as individuals in overwintering North American monarch colonies. (c) The larva of a *Euploea* species; only the adult stage overwinters. (d) A *Euploea* pupa. (e) *Ideopsis similis similis* female nectaring on a flower in a colony on a warm day in late January. (f) *Euploea mulciber barsine* adult nectaring on a flower at an overwintering site in early December. (g) A mimetic nymphaline, *Hypolimnas bolina kezia* (Butler) female, here seen drinking water at a stream in a danaine colony site, may also overwinter in the adult stage, but any migratory behavior is unknown. (h) *Euploea* males evert yellow androconial brushes from their abdomens at times while flying at mid-day in an overwintering colony. (i) *Tirumala hamata septentrionis* male nectaring at a flower in an overwintering valley. (j) *Danaus genutia genutia* male visiting a flower in December in a colony. (k) *Euploea sylvester swinhoei* male. (l) *Euploea eunice hobsoni,* male. (m) *Euploea eunice hobsoni,* female. (n) *Euploea tulliolus koxinga,* male. (o) *Euploea mulciber barsine,* male. (p) *Euploea mulciber barsine,* female. (q) *Euploea tulliolus koxinga,* female.

In some of the valleys, the aggregations get so dense that twigs, branches, and leaves are covered with danaines perched shoulder-to-shoulder. Even the green color of the foliage is replaced by the predominantly black color of the underside of the wings. On warm nights, the overwintering danaines can be attracted off their perches by electric lights or flashlights, many of them flying just like moths around the light source.

Wang (unpublished) has noted that, at least in *Euploea tulliolus koxinga,* males evert and display their brushes of yellow hair pencils from their abdominal tips (Plate 1:h) while flying around at the overwintering sites in early February, before any courtship and mating activity is observed. He postulates that the pheromones of these *Euploea* may play an important role as an aggregation stimulus for the overwintering danaines, in addition to their role at other times of the year in courtship and mating.

As the warmer weather of March comes, the overwintering danaines become more and more active, leaving the roost daily for water and nectar (Plate 1:a). In late March, the butterflies begin courting and mating, and soon after mating, the females begin to fly north, back to the high elevation breeding areas in the northern parts of the island. Presumably, males die within a short time after mating. The departure from the overwintering sites is gradual, in striking contrast to the mass arrival during the fall.

DISCUSSION

The most important point of this report is that the monarch is not unique among the Danainae in its migration and over-wintering behavior. The fact that other members of the Danaini, and Euploeini, show similar behaviors suggests that it is a well-established ancestral trait in the Danainae in general.

The regular southward and northward migratory behavior and overwintering aggregations of the Monarch, *Danaus plexippus,* in response to cold weather has been well documented on the continent of North America (e.g., Williams 1930, 1958, Urquhart 1960, 1987, Brower 1977, 1985, Calvert & Brower 1981, Ackery & Vane-Wright 1984). Otherwise, few studies have been done on danaine migrations and overwintering behavior, although this behavior may be widespread in the subfamily as a response to either cold or dry seasons. Some observations of dry-season movements of neotropical danaines through mountain passes in Venezuela and Costa Rica have been reported (Beebe 1950, DeVries 1987). Scattered observations of migrations of certain species in the genera *Danaus, Tirumala, Parantica, Ideopsis,* and *Euploea* have been made in East Africa, southern India, and Sri Lanka (Ackery & Vane-

Wright 1984). A detailed study of a subtropical, locally-overwintering aggregation of the common crow butterfly, *Euploea core corinna* (W. S. Macleay), has been made in Brisbane, Australia (Kitching & Zalucki 1981). In addition to this Indo-Australian danaine species, winter aggregations (May–September) are recorded for the dry season in northeastern Australian populations of *E. sylvester* (F.) and *E. tulliolus* (F.), *Tirumala hamatus* (W. S. Macleay), and *Danaus affinis* (F.). *Euploea core* is capable of living as long as 160 days, but it is not migratory (Kitching & Zalucki 1981), unlike the nine danaines (including four *Euploea* species) in Taiwan and *Danaus plexippus* in North America.

The observations reported here show that there are still many questions to be answered about these migrations in Taiwan. The details of the migratory route are unknown, especially during the early parts of the movement from the northern and central parts of the island to the southern higher mountain areas, prior to the movement downhill to the low-elevation valleys. Additional locations of overwintering sites are certain to be found with further searching. Detailed studies need to be made of the relation between climatic and weather conditions and the particular overwintering locations chosen by these danaids, similar to the work that has been done by Lincoln P. Brower (e.g., 1977, 1985) and his colleagues (e.g., Calvert & Brower 1981) in the overwintering sites of *Danaus plexippus* in central Mexico. The permanence of the overwintering sites needs to be ascertained, although all observations to the present indicate that the same sites are used year after year.

It is known that the nine migratory species of danaines in Taiwan have two to four generations a year (Hamano 1986). The adult danaines of the summer season live only about one month, but the overwintering adults of these species can live about six months, from October to at least March of the following year. All nine species of overwintering danaines share the characteristic of having a very tough integument that makes them difficult to kill (as tested by squeezing the thorax between thumb and forefinger). It is also relatively difficult to rub the scales off these butterflies. It would be valuable to test the palatability of these danaines to insectivorous birds and other potential predators in both the summer ranges and the overwintering sites.

Additional unanswered questions include: Are there any overwintering valleys along the eastern side of the Central Mountain Range in addition to the recently discovered one in Taiton County at Dawu? Is the true migratory route in the western plains area actually along the coastline, or over the sea itself? Do the danaines that come from the northern part of Taiwan congregate in the same valleys as those that come from the mountains in the southern part of Taiwan?

Expanded research on the overwintering danaines of Taiwan should

generate fascinating comparative material for those interested in studying and preserving the tremendous overwintering aggregations of the Monarch (*Danaus plexippus*) in North America. In the meantime, preserving the very few overwintering sites of danaine butterflies in Taiwan will be of the greatest importance for conservationists in that country, and, indeed, for lepidopterists and others around the world who may wish to travel to see these great natural phenomena for themselves. The aggregations offer great potential for winter tourism in Taiwan, and perhaps admission fees could be collected to help defray protection costs. Currently, the sites occupied by the colonies are only marginally attractive for agricultural clearing and development, but that could change with increasing population pressures.

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