

NOTES ON THE LIFE CYCLE AND NATURAL HISTORY
OF BUTTERFLIES OF EL SALVADOR. IIC.
SMYRNA BLOMFILDIA AND *S. KARWINSKII*
(NYMPHALIDAE: COLOBURINI)

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ABSTRACT. Descriptions and photographs of the life histories of *Smyrna blomfildia* and *S. karwinskii* are presented, and the larval foodplants (Urticaceae) and the comparative behavioral characteristics of the two species are recorded and discussed. The present taxonomic placement of *S. blomfildia* and *S. karwinskii* is questioned, and an alternate interpretation is expressed based on the differing degrees of morphism between the two species. The adaptiveness of polymorphism is explained relative to human-disturbed habitats in El Salvador, noting that the monomorphic *S. karwinskii* is the most evolved species, but that *S. blomfildia* has a flexibility to overcome adverse conditions because of certain polymorphic characteristics. The peculiar phenomenon of a divergent evolutionary trend between the early stages (larvae and pupae) and an advergert trend between the adults of both species is noted.

This is the second of three papers on the Coloburini (Gynaeciini) of El Salvador. Classically, *Colobura dirce* L. and *Historis odius* Fab. have been included with *Smyrna* in the Coloburini, based, no doubt, on similarities in adult characteristics. Whether or not these form a natural complex of related species is left for others to determine, who can compare the overall characteristics of *Smyrna* sp., *Colobura dirce*, and *Historis odius*.

We present here a description of the early stages of *Smyrna blomfildia* Fab. and *S. karwinskii* Hübn., records of the larval foodplants, and an account of the behavior observed in both the immatures and adults. We have reared *S. blomfildia* and *S. karwinskii* using the same techniques described for the Catonephelini, Charaxini, and Hamadryadini (Muysshondt, 1973a, 1974b; Muysshondt & Muysshondt, 1975a) with consistently uniform results. Specimens preserved in alcohol have been sent to the American Museum of Natural History, New York City.

Life Cycle

Smyrna blomfildia

Egg. Almost spherical with flattened base, light green with 10 whitish vertical ribs which fade around the micropyle. Ca. 1 mm diameter. Hatches in 5 days.

Smyrna karwinskii

Same as *S. blomfildia* in all respects.

1st instar larva. Head roundish, naked, shiny black. Body naked, cylindrical, brownish-green, with transverse rows of white, shallow, small warts on each segment. Legs and tips of prolegs dark brown. Ca. 2 mm when hatched, growing to 4.5 mm in 2 days.

2nd instar larva. Head shiny black, with short, knobby, divergent horns, one on each epicranium, and 8 small, white conical projections across head capsule, under epicranial horns. Body brown with transverse rows of tiny, forked spines implanted on white chalaza. Grows to 8 mm in 2 days.

3rd instar larva. Head reddish with thick, short horns (ca. head length) armed with secondary spines placed in the following order: a basal row of 3, 1 pointing inwards, 2 anterad; a second row, with 1 pointing caudad, 1 anterad and 1 laterad. Horns terminate distally in a club with 5 short spines. Around base of each horn are 7 spines; around the ocelli are 5 smaller spines. Body predominantly dark brown with some light spots among the spines, which are placed in the following positions: 1st thoracic segment (T-1) with 1 spine subdorsally, 1 subspiracular spine and 1 pedal spine. T-2 and T-3 with 1 subdorsal scolus with a rosette of 5 spines near tip and 1 vertically; 1 supraspiracular scolus with rosette of 4 spines and 1 vertical; 1 subspiracular spine and 1 pedal spine. Abdominal segments from A-1 to A-7 have, in addition, 1 dorsal scolus with 2 lateral spines and 1 distal, and behind the subspiracular spine 1 scolus with rosette of lateral spines and 1 distal spine. A-1, A-2 and A-7 have 1 small ventral spine in line with prolegs. A-8 has an additional scolus caudad with a 6-spined rosette. A-9 with only 1 subdorsal scolus directed posterad with rosette of 5 lateral spines and one distal. A-10 with anal shield and 2 lateral groups of small spines directed posterad. Grows to 15 mm in 2 days.

4th instar larva. Same as 3rd instar but body shows various color morphs: 1 dorsally brown with cream dots, rest of body cream also, where black spiracula

Same as *S. blomfildia*, but light green with transverse rows of white warts.

Same as *S. blomfildia*, but body lighter color and lacking dorsal spines in all but 8th abdominal segment.

Head light brown with longer and thinner horns than *S. blomfildia* ($1\frac{1}{2}$ head length). Lateral spines of head much reduced. Horn terminals more clubbed. Body color basically brown with double transverse rows of whitish dots on each segment and a broken stripe of light color subspiracularly. Spiracula black. Ventral surface dirty light gray, prolegs beige. Body with whitish scoli armed with concolored black-tipped spines, placed in the following order: T-1 with subdorsal group of 3 small spines, then 1 small supraspiracular spine, 1 small subspiracular spine and 2 small pedal spines. T-2 and T-3: 1 subdorsal scolus, short, with rosette of 6 lateral spines and 1 distal spine; 1 supraspiracular scolus with rosette of 5 lateral spines and 1 distal; 1 subspiracular spine and 2 pedal spines. Abdominal segments A-1 and A-7 have a subdorsal scolus with a rosette of 4 lateral spines and 1 distal; supraspiracular scolus with rosette of 4 lateral spines and 1 distal; subspiracular scolus with 4 lateral spines and 1 distal, then two small pedal spines. A-8 has in addition a heavier dorsal scolus armed with 8 spines. A-9 has only 1 supraspiracular scolus directed posterad, with 6 spines. Anal plate on A-10 surrounded by 6 small spines. Grows to 15 mm in 2 days.

Head dirty yellow, with some brown markings frontally. Slender horns, slightly bent in some individuals, colored light gray. All head and horn spines white with

stand out and all scoli and spines whitish. Another morph mostly black dorsally, with double row of whitish dots along meson. From supraspiracular to ventral area cream colored. Dorsal scoli white, subdorsal and supraspiracular scoli black, the rest whitish. Other morph mostly greenish-white with black stripes covering dorsal and subdorsal area, but much broken by stripes and dots of greenish-white. All scoli greenish-white with light spines. Still another morph similar to the preceding one but with subdorsal and supraspiracular scoli black. The rest whitish. Grows to 28 mm in 2 to 3 days.

5th instar larva. Same as 4th instar, growing to 41 mm in 3 to 4 days.

Prepupa. No noticeable change. Hangs from anal prolegs, body incurved ventrally. Lasts 1 day.

Pupa. From light brown to very dark brown, abdominal segments darker than the rest, with rows of lighter, shallow warts: 1 supraspiracularly, 1 subspiracularly. Spiracula inconspicuously brown. One black spot at either side between wingcase and thorax. Abdomen rounded with no sharp angles; slightly incurved ventrally, shallow depression at the thoracic union dorsally. Thorax slightly keeled to rounded head. Pointed cremaster dark brown. 25 mm long, 10 mm laterally and dorsoventrally at widest points. Adults emerge between 8–11 days.

Adults. Both species show a marked sexual dimorphism in the coloration, males being brighter than females. Wing shape is the same in both sexes.

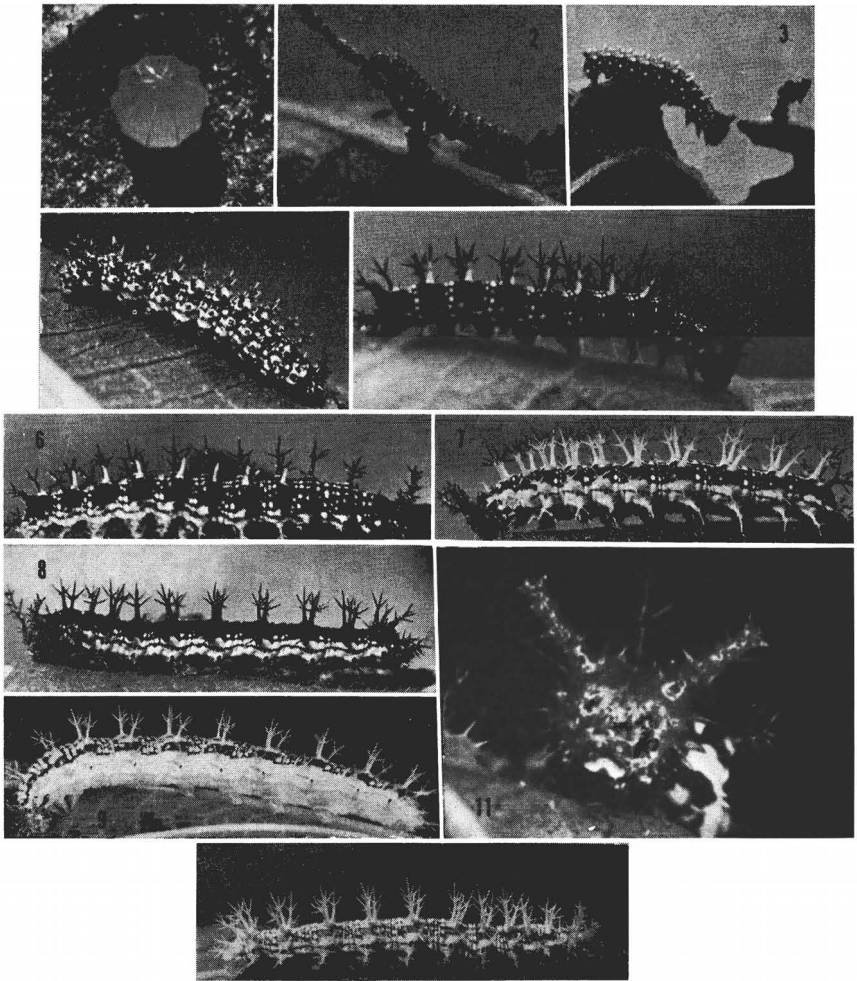
Males. Dorsally forewing golden brown in basal and discal areas with lighter golden-orange band slanting from midcostal margin to tornus. (*S. blomfieldia* tends to be lighter than *S. karwinskii*.) The rest velvety black, except a subapical row of three, light yellow spots parallel to the light band. Hindwing in *S. karwinskii* golden-brown mostly, with a black edge along outer margin, 3 mm wide, near outer angle, very thin from there down along the very edge of the wing to anal angle. A submarginal row of faint black dots along the thin portion of the black edge. In *S. blomfieldia* hindwing is a lighter golden-orange and black edge along outer angle becomes submarginal along

black tips. Body ground color light gray with a darker thin mesal stripe, and transverse rows of cream colored spots at segment unions. All scoli as in 3rd instar, implanted now on bright yellow chalaza; scoli and spines white with black tips. Grows to 29–30 mm in 2 to 3 days.

Drastic change in color. Now mostly brown with black markings on head, between dark horns and down to ocelli laterally. The whole body with black irregular marblings. All scoli shorter than in prior instars; brown colored as well as spines, legs and prolegs. Grows to 40–42 mm in 3 to 4 days.

Same as *S. blomfieldia*. 1 day.

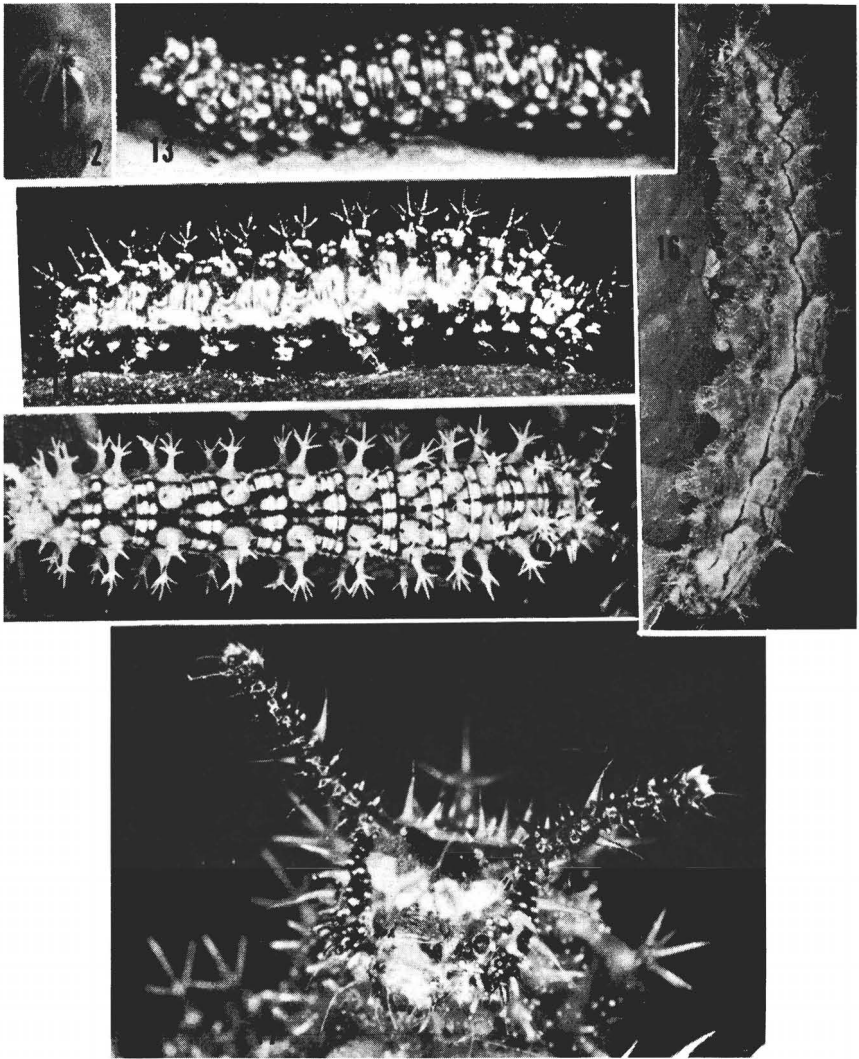
Lighter brown and thinner than *S. blomfieldia*. Abdomen more humped dorsally and with 3 rows of conical spines: 1 prominent subdorsally, 1 of decreasing size supraspiracularly, and 1 still smaller subspiracularly. Thoracic dorsal keel sharply angled midways. Black spots between wingcase and thorax, as *S. blomfieldia*. Black pointed cremaster set at an angle in relation to body plan. 28 mm long, 11 mm dorsoventrally, 10 mm laterally at widest points. Lasts 9–11 days.



Figs. 1-11. *Smyrna blomfieldia*: 1, egg, recently deposited, 1 mm; 2 (photo upside-down), 1st instar larva, 4.5 mm (note "perch" on central vein); 3, 2nd instar larva, 8 mm (note new "perch" being constructed at edge of leaf); 4, 3rd instar larva, 15 mm; 5, 4th instar larva, 28 mm; 6-10, 5th instar larvae, various morphs, 41 mm; 11, 5th instar larva, close-up of head.

outer margin down to M_2 where it becomes thin, ending between Cu_1 and Cu_2 where it is substituted by a marginal thin edge running between the two, small toothed projections on anal angle, with a whitish dot in the interior one. Inner fold in both species fulvous gray.

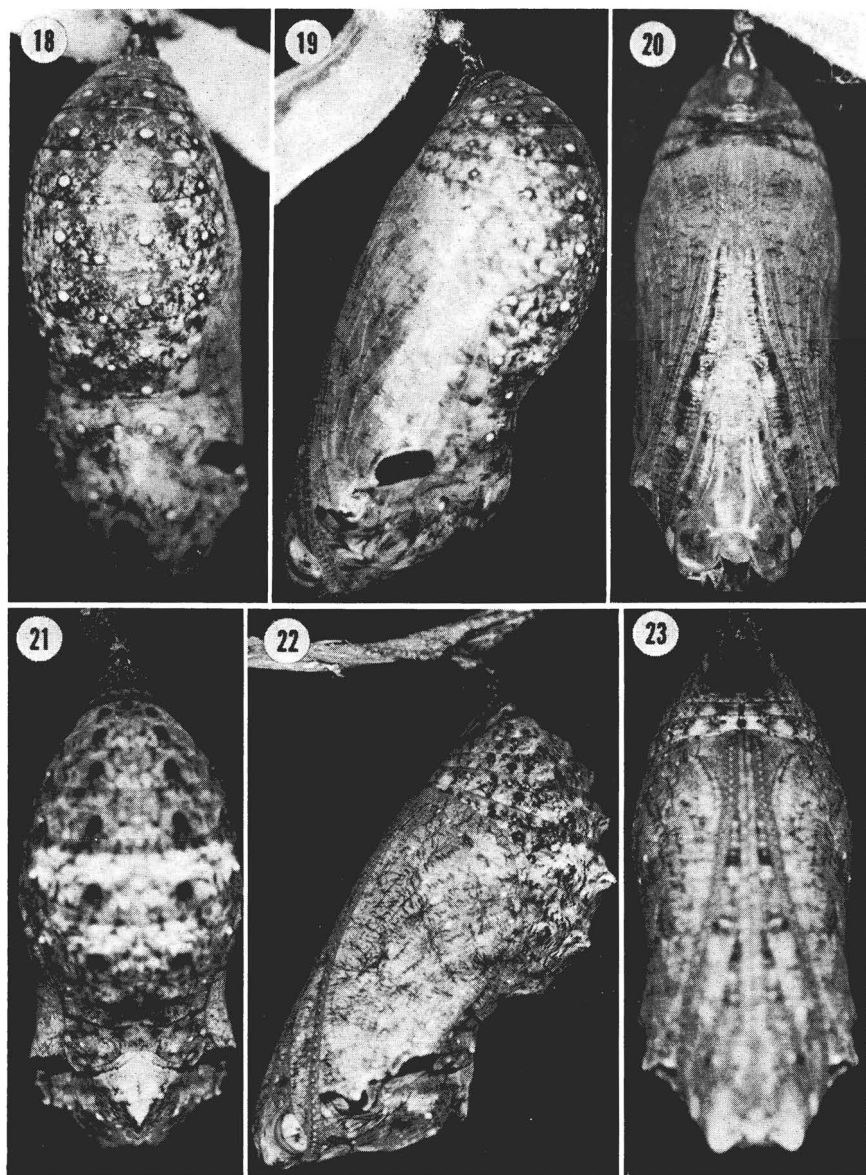
Ventrally forewing presents basally some black drawings, on light yellow basic color, which is devoid of markings from midcostal margin to tornus, except for a brownish gray border along inner margin, more so in *S. karwinski*. From midcostal to subapical costal margin down to mid-outer margin to tornus there is a black zone



Figs. 12–17. *Smyrna karwinskii*: 12, egg, ready to hatch, 1 mm; 13, 1st instar larva, 3.5 mm; 14, 3rd instar larva, 15 mm; 15, 4th instar larva (note absence of dorsal spines and slender horns), 29–30 mm; 16, 5th instar larva (note reduced scoli), 40–42 mm; 17, 5th instar larva, close-up of head.

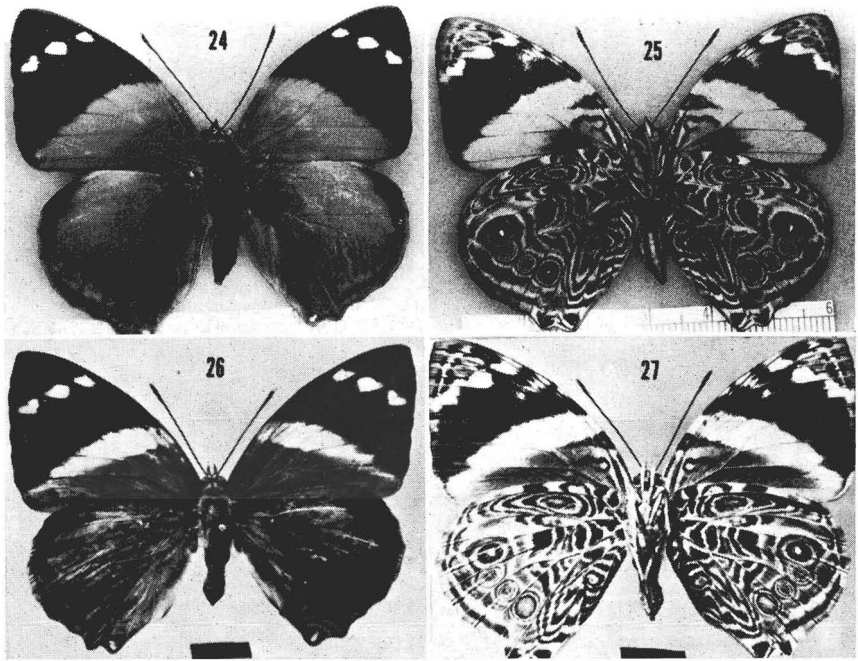
limited distally by a diffuse replica of the dorsal subapical dots, which ventrally merge with each other. Apically a gray zone mottled by faint black markings, more contrasting in *S. blomfieldia* than in *S. karwinskii*.

Hindwings show a complicated pattern of sinuous lines, circles and triangles of dark brown, light brown and whitish color, all darker in *S. blomfieldia* than in *S. karwinskii*.



Figs. 18-20. *Smyrna blomfieldia*: 18, dorsal view of pupa; 19, side view of pupa; 20, ventral view of pupa.

Figs. 21-23. *Smyrna karwinskii*: 21, dorsal view of pupa; 22, side view of pupa; 23, ventral view of pupa.



Figs. 24–27. *Smyrna blomfildia*: 24, dorsal view of male; 25, ventral view of male (metric scale); 26, dorsal view of female; 27, ventral view of female.

Both species present a submarginal row of 4 “eyes” along outer margin, the two at the extremes twice as large as the two interior ones. Both species also have a black spot on the anal angles. *S. blomfildia* in addition has a second black spot on the first toothed projection.

Females. Both species dorsally have the same pattern as the males, but the golden-brown or orange is replaced by dull brown, separated from the black apical area by a light yellow band. The rest as in males and so is the underside of the wings.

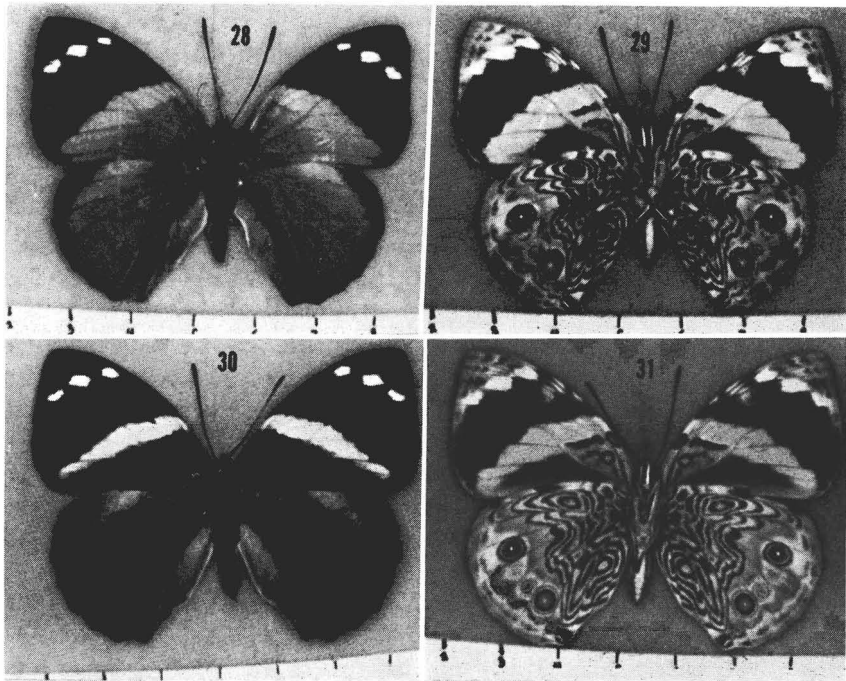
Body is concolorous to the respective wing coloration. Antennae black, ending with an orange tip, larger in *S. blomfildia*. Palpi cream colored, proboscis tanned brown. Wing span 70–80 mm. *S. blomfildia* usually larger than *S. karwinski*, and females larger than males, more markedly so in *S. blomfildia*.

Total time from egg to adult, 25–30 days.

Natural History

Females of both species of *Smyrna* deposit their solitary eggs on the undersides of leaves of various *Urticaceae*. In contrast, other species of *Coloburini* oviposit on *Moraceae*. We have found the eggs of both *Smyrna* spp. on *Urticastrum mexicanum* (Ieb.) Kuntze, *Urera caracasana* (Jacquin) Grisenbach, and *U. baccifera* (L.) Gaudichaud.

The fast flying females land on the undersurfaces of leaves for ovi-



Figs. 28–31. *Smyrna karwinskii*: 28, dorsal view of male (note absence of indentations in anal angles); 29, ventral view of male; 30, dorsal view of female; 31, ventral view of female.

position. This is in striking contrast to the rest of the Coloburini we have been able to study, which oviposit mostly on the upper surface of leaves. Female *Smyrna* quickly deposit one egg, then move to another plant close by where the process is repeated. It is not uncommon for the same plant to be visited again after a period of time. We have observed that females deposit more than five eggs in sequence before moving away. The plants used are generally less than 3 m tall.

The rather small eggs are quite hard to locate, due in part to the stinging properties of the plants, but also to the light green color of the eggs, which makes them inconspicuous against the color of the leaves. After 5 days the larva hatches and consumes most of the eggshell, leaving traces of the wall. It proceeds to feed on the undersurface of the leaf, where it constructs a resting perch very close to its feeding place, perpendicular to the surface. This is a notable deviation from the usual method of the other perch-making species we know, which always move to the edge of a leaf to feed, and which construct their resting perch by prolongation of a vein. In *Smyrna* spp., second instar larvae do eventually construct the

perch at the edge of the leaf. From then on, the larvae remain on the undersurface of leaves until pupation. They pupate on the same plant, either under leaves or on petioles, after hanging by the anal prolegs for one day with the thoracic segments incurved ventrally. The pupa hangs loosely from the pointed cremaster, swinging freely with the faintest movement of the plant. The colors of the wings of the pharate adult do not show through the wingcase of the pupal skin when the adult insect is ready to emerge, due to the dark color of the pupa. After emergence, a rusty-colored meconium is ejected while the insect expands its wings. The imago takes a long period of time before its first flight.

Both species show marked sexual dimorphism. At the same time, the two species are very similar to one another dorsally. The principal difference is that *S. karwinskii* has a rounded anal angle on the hindwing, where *S. blomfieldia* has a small toothed projection.

We have never seen imagos of either species visiting flowers, but we have seen them feeding on sap flowing from tree wounds, fermenting fruits, mud puddles, etc., where they spend long periods of time, with their wings folded dorsally.

Smyrna karwinskii is noteworthy for its seasonal gregarious roosts in high mountains during the dry season (Muysshondt & Muysshondt, Jr., 1974). This phenomenon also occurs in Mexico (R. Wind, Chiapas, pers. comm.; Beutelspacher, 1975). We have never found eggs or larvae of *S. karwinskii* in the high mountains during the dry or the rainy season, even where the foodplants occur locally. It seems that they move down to lower levels to breed, usually in close proximity to *S. blomfieldia*. The latter very seldom is found at altitudes over 1600 m and does not have the communal roosting behavior of *S. karwinskii*. It is not uncommon to collect eggs and larvae of both species on the same plant.

The adults of both species behave similarly: they have the same fast rustling flight, they perch on tree trunks with their heads pointing down, and the males have a strong territorial defensive attitude, chasing intruding butterflies of the same or different species.

To date we have not found cases of parasitism in these species, but we have very often witnessed predation by Hemiptera (Reduviidae, mostly) which impale the larvae, leaving only the sagging skin. Another cause of severe larval mortality in the fields is a disease causing the larva's body to burst, releasing a foul-smelling dark fluid.

The foodplants, known locally under one vernacular name common to the three species, "Chichicaste," are plants often used as hedges around coffee plantations, because of the severe stinging caused by the leaves which deters trespassers.

Urera baccifera grows to a height of 7 m when left alone. The trunks

and older branches are covered with short, wide spines, the younger branches and the leaves with stinging hairs. The leaves are large, coarse, round-cordate and roughly dentate. The small greenish flowers grow in cymes, producing small, translucent, globose fruits with a dark seed inside. These fruits are much sought after by farm children, who pick them by beating the shrub with a stick while catching the rain of falling fruits with a "sombbrero." Thus, hundreds are collected before disposing of them *in situ*, much to their pleasure. The juicy fruits have a sweetish-refreshing taste and alleviate thirst readily.

Urera caracasana grows to about 4 m and is also used in fences. The leaves are smaller, and of variable shapes; more or less elongate, cordate at the base and acute at the apex, with close dentation at the edges. The fruits are red when mature. Both species are used in popular medicine against venereal diseases. *Urticastrum mexicanum* is a shrub up to 4 m tall, with ovate, crenate leaves. The fruits are achenes. All of these plants have caused painful accidents to tourists unaware of the severe stinging properties of the otherwise handsome leaves.

DISCUSSION

Smyrna blomfieldia is the type-species of the genus *Smyrna* Hübner, based on the butterfly originally named *Papilio blomfieldia* by Fabricius in 1781 (Hemming, 1967). As he very often did, Hübner misspelled the specific name as "blomfildii," and this erroneous spelling was subsequently used by several authors, among them Herrich-Schäffer (1864) and Müller (1866), with an additional error: "blomfieldii." Other authors named the species *S. bella* Godart and *S. pluto* Westwood (Seitz, 1921).

The only other reports of the early-stages of this genus that we are aware of are by Müller, who gave a short description of a probable 4th instar larva preserved in alcohol, some rough descriptions based on that of Müller's (Seitz, 1921; Hayward, 1964), and a vague comparison between the larvae of *Colobura* and *Smyrna* by Brown & Heineman (1972). We believe that ours is the first complete description of the early stages, with photographic illustrations of both *Smyrna blomfieldia* and *karwinskii*.

The genus *Smyrna* has been placed in various unrelated groups based mostly on the external characters of the perfect insects by many early authors. Doubleday, Westwood and Hewitson (1849) and Boisduval (1870), placed it close to *Agrias*. Herrich-Schäffer (1864) put this genus in his "familie XI," together with the related genera *Gynaecia* and *Callizona*, and many unrelated ones, among them *Euptoieta*, *Eunica*, *Pyrrhogyra*, *Ageronia*, *Peridromia*, *Amphichlora*, etc. Schatz & Röber (1892), placed *Smyrna* in their "Gynaecia-Gruppe," as part of their

larger "Eunice-Gruppe," together with *Callizona* and *Gynaecia* (*Colobura*), probably following Herrich-Schäffer.

Today, many authors follow Seitz (1921), who was probably influenced by Reuter (1898) in placing *Smyrna* in his "Gruppe Gynaeciidae," together with *Historis*, *Coea*, *Pycina*, *Megistanis*, *Gynaecia* and *Callizona*, as an intermediate group between his "Gruppe Epicaliidi" including many genera (*Catonephele*, *Epiphile*, *Temenis*, *Pseudonica*, *Pyrrhogyra*, etc.) covered by one of us (Muysshondt, 1973a, b, c, d; 1974a) in previous papers and his "gruppe Hypolimnadidi," with *Hypolimnas misippus* L. Other modern authors include this genus and related genera (*Historis*, *Coea*, *Colobura*, etc.) in the Limenitidini which we believe is erroneous.

Different opinions arise, no doubt because of superficial similarities of the adults, which could very well be due to convergent evolution rather than close relationship. Examples are well known of convergence in color, pattern, and shape between unrelated species actually belonging to different families: i.e. Danaidae, Ithomiidae, Heliconiidae and Pieridae. These often form Müllerian and Batesian mimicry complexes, as pointed out by many biologists (Brower, 1972; Brown & Benson, 1974).

The very poor knowledge of the immatures of most tropical butterflies has led to errors in the association of species. Descriptions of the immature stages are necessary for a more accurate systematic arrangement of the neotropical Lepidoptera.

Comparison of the eggs of the two species of *Smyrna* indicates that they are very closely related. Larvae and pupae are also very similar, although the larvae of *S. karwinskii* lack the dorsal row of scoli present in *S. blomfieldia*. In contrast, the eggs, larvae and pupae of *Smyrna* differ considerably from those of *Colobura dirce*. The immature stages of *Historis odius* and *Coea acheronta* resemble each other closely, but have nothing in common with *Colobura*, and only the larval head shape resembles *Smyrna*.

There are so many drastic differences between the characteristics of the early stages of the species of Coloburini studied by us [*Colobura dirce* L. (Muysshondt, Jr. & Muysshondt, 1976), *Historis odius* (Fab.) and *Coea acheronta* (Fab.), (Ms. in prep.)], that we question the correctness of the taxonomy of the group.

However, we feel that although *Smyrna* is an aberrant genus in the Coloburini, it represents a link between the Nymphalini and the other genera now included in the Coloburini.

By the same token it is also evident that none of these species can be placed in the Charaxinae, as was done by Boisduval (1870), who placed *Smyrna* between *Agrias* and *Prepona*, and said that the larvae of

Aganisthos (= *Historis*) and *Prepona*, "sont tout-à-fait semblables" (exactly alike). This is absolutely incorrect! *Prepona* and *Archeoprepona* do resemble each other in the shape of the eggs, larvae and pupae (Muysshondt, 1973e; Muysshondt, 1976), but neither stage resembles even remotely the early-stages of *Historis* (Ms in prep.). To include *Smyrna* with the Limenitidini (in which *Adelpha* belongs) as most modern authors do, is also incorrect, as they have nothing in common with the Coloburini during their early stages. With Limenitidini there are certain imaginal resemblances, but these are not strong enough to place them together.

It is noteworthy that the larvae of both species of *Smyrna* construct a resting perch with frass pellets. Other larvae which use this defensive strategy construct their perch at the edge of the leaf on which they live: some of them pile a barrier of excreta mixed with pieces of dry leaf tissue at the base of the perch (*Adelpha* spp.); some fasten leaf cuttings with silk which hang from the perch (*Zaretis*, *Prepona*, *Archeoprepona*); many others leave the perch bare (*Biblis*, *Mestra*, *Catonephele*, *Epiphile*, *Nica*, *Temenis*, *Pyrrhogyra*, *Diaethria*, *Catagramma*, *Cyclogramma*, *Hamadryas*, *Colobura*, *Historis*, *Coea*, *Apatura*, *Marpesia*). As far as we have been able to ascertain only the two species of *Smyrna* construct a perch on the underside of a leaf, very close to where the eggshell was consumed. During the 2nd instar, a new perch is sometimes made at the edge of the leaf; the other species mentioned also do this. We interpret this behavior to result from protection afforded to the small larvae by the strong urticating properties of the foodplants, a factor which by itself might deter at least some predators. After the 2nd instar the larvae abandon their perch and wander about the plant on the underside of the leaves. Perhaps the urticating properties of the plant afford continued protection. It is to be noted that the profusion of spines displayed by the larvae of *Smyrna* spp. from the 3rd instar on do not have urticating properties. Even the ventral prothoracic gland (adenosma), is not readily extruded as in *Colobura dirce* and other species provided with this apparent means of defense. Thus, it seems that the larvae of *Smyrna* rely on the protection granted by the plant itself, rather than on the protection they could derive from their own spines and odoriferous gland.

One thing puzzles us: although the adults of the two species of *Smyrna* are strikingly alike, why is it that the larvae and even pupae of the two species show important differences, such as the unequal number of rows of scoli in the larvae, and the different shape of the pupae?

We have seen various larvae and pupae of species belonging to the same genus, the adults having a common shape but with very disparate

coloration, such as *Siproeta stelenes* (Young & Muysshondt, 1973) and *V. epaphus* (Young, 1972), *Heliconius petiveranus* and *H. charitoni*; *Anartia fatima* and *A. jatrophae*. Still others show differences not only in color, but in the shape of the wings of the adult, as do *Catonephele numilia* and *C. nyctimus*. Yet the larvae and pupae, except for minor discrepancies, if any, have the same characteristics, indicating that they undoubtedly both belong to the same genus. We have seen, on the other hand, species placed in the same genus which have very basic differences during their early stages, for example *Hamadryas februa*, *H. guatemalena* and *H. amphinome*; and *Anaea eurypile*, *A. morvus* and *A. pithyusa*, suggesting that they may belong to different but related genera of one subfamily or family (Muysshondt & Muysshondt, Jr., 1975a, b, c; Muysshondt, 1974b, 1975a, b). For these reasons, regardless of the striking resemblances in adult coloration and shape between *Smyrna blomfildia* and *S. karwinskii*, we suggest they might belong to different genera. They would then form another case of evolutionary convergence, perhaps of Müllerian mimicry. While *S. blomfildia* seems to be in the process of finding its optimum larval characteristics, as suggested by the striking polymorphism in larval coloration, *S. karwinskii* apparently has already achieved stability as it has only one morph. We consider *S. karwinskii* as the most evolved of the two, because of the uniformity of characteristics maintained during its whole life cycle, and thence the model of the two. *S. blomfildia* we consider to be the youngest, still an evolving species. This evolutionary phase seems to have momentarily given *S. blomfildia* an advantageous flexibility to overcome adverse conditions which are reflected in a more abundant population than its more stable relative, *S. karwinskii*, at least under the conditions in El Salvador where the habitats are continuously and severely affected by human influences, due to the high population density.

It would be interesting to read an explanation of the present phenomenon, where two species evolve divergently during their early stages, yet seem to evolve advergently during their adult stage. Most of the work of which we are aware on the evolution of butterflies has concentrated on their adult stage, disregarding almost completely their early stages, which perhaps would throw new light on the problem.

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LITERATURE CITED

- BEUTELSPACHER, C. R. 1975. Notas sobre el suborden Rhopalocera (Lepidoptera) de las Minas, Veracruz. Rev. Soc. Mex. Lep. A. C. 1(1): 11-20.
- BOISDUVAL, J. 1870. Considerations sur des Lépidoptères envoyés du Guatemala à M. de l'Orza. Rennes.
- BROWER, L. P. & J. VAN ZANDT BROWER. 1972. Parallelism, convergence, divergence and the evolution of mimicry. Trans. Conn. Acad. Arts Sci. 44: 59-67.
- BROWN, F. M. & B. HEINEMAN. 1972. Jamaica and its butterflies. E. W. Classey, Ltd. London. 478 p.
- BROWN, K. S. & W. W. BENSON. 1974. Adaptive polymorphism associated with multiple Müllerian mimicry in *Heliconius erato* (Lepid.-Nymph.). Biotropica 6: 205-228.
- DOUBLEDAY, E., J. O. WESTWOOD & W. C. HEWITSON. 1849. The genera of diurnal Lepidoptera. Vol. 2. Longman, London.
- HAYWARD, K. J. 1964. Genera et species animalium Argentinarum. Vol. 3. Insecta, Lepidoptera, Familiae Nymphalidearum. Universitas Nationalis Tucumanensis, Fundatio Michaelis Lillo. Kraft Ltd., Buenos Aires.
- HEMMING, F. 1967. The generic names of the butterflies and their type species. (Lepidoptera: Rhopalocera). Bull. British Mus. (Nat. Hist.), Entomology Suppl. 9. 509 p.
- HERRICH-SCHÄFFER, G. A. 1864. Prodrömus Systematis Lepidopterorum. Korres. Blatt Zool.-min. Ver. Regensburg, 18.
- MÜLLER, W. 1886. Südamerikanische Nymphalidenraupen. Versuch eines natürlichen Systems der Nymphaliden. Zool. Jahrb. Zeitschr. Syst., Geogr., Biol. Thiere 1: 417-678.
- MUYSHONDT, A. 1973a. Notes on the life cycle and natural history of butterflies of El Salvador. IA. *Catonephele numilia* Esite (Nymphalidae-Catonephelinae). J. N. Y. Entomol. Soc. 51: 164-174.
- . 1973b. Notes on the life cycle and natural history of butterflies of El Salvador. IIA. *Epiphile adrasta adrasta* (Nymphalidae-Catonephelinae). J. N. Y. Entomol. Soc. 51: 214-223.
- . 1973c. Notes on the life cycle and natural history of butterflies of El Salvador. IIIA. *Temenis laothoe liberia* (Nymphalidae-Catonephelinae). J. N. Y. Entomol. Soc. 51: 224-233.
- . 1973d. Notes on the life cycle and natural history of butterflies of El Salvador. IVA. *Pseudonica flavilla canthara* (Nymphalidae-Catonephelinae). J. N. Y. Entomol. Soc. 51: 234-242.
- . 1973e. Notes on the life cycle and natural history of butterflies of El Salvador. I. *Prepona omphale octavia* (Nymphalidae). J. Lepid. Soc. 27: 210-219.
- . 1974a. Notes on the life cycle and natural history of butterflies of El Salvador. VA. *Pyrroggyra hypsenor* (Nymphalidae-Catonephelinae). J. N. Y. Entomol. Soc. 52: 163-172.
- . 1974b. Notes on the life cycle and natural history of butterflies of El Salvador. IV. *Anaea (Memphis) eurypyle confusa* (Nymphalidae). J. Lepid. Soc. 28: 306-314.
- . 1975a. Notes on the life cycle and natural history of butterflies of El Salvador. V. *Anaea (Memphis) morvus boisduvali* (Nymphalidae). J. Lepid. Soc. 29: 32-39.
- . 1975b. Notes on the life cycle and natural history of butterflies of El

- Salvador. VI. *Anaea (Memphis) pithyusa* (Nymphalidae). J. Lepid. Soc. 29: 168-176.
- . 1976. Notes on the life cycle and natural history of butterflies of El Salvador. VII. *Archaeoprepona demophon centralis* (Nymphalidae). J. Lepid. Soc. 30: 23-32.
- MUYSHONDT, A. & A. MUYSHONDT, JR. 1974. Gregarious seasonal roosting of *Smyrna karwinskii* adults in El Salvador (Nymphalidae). J. Lepid. Soc. 28: 224-229.
- . 1975a. Notes on the life cycle and natural history of butterflies of El Salvador. IB. *Hamadryas februa* (Nymphalidae-Hamadryadinae). J. N. Y. Entomol. Soc. 53: 157-169.
- . 1975b. Notes on the life cycle and natural history of butterflies of El Salvador. IIB. *Hamadryas guatemalena* (Nymphalidae-Hamadryadinae). J. N. Y. Entomol. Soc. 53: 170-180.
- . 1975c. Notes on the life cycle and natural history of butterflies of El Salvador. IIIB. *Hamadryas amphinome* (Nymphalidae-Hamadryadinae). J. N. Y. Entomol. Soc. 53: 181-191.
- MUYSHONDT, A., JR. & A. MUYSHONDT. 1976. Notes on the life cycle and natural history of butterflies of El Salvador. IC. *Colobura dirce* L. (Nymphalidae-Coloburinae). J. N. Y. Entomol. Soc. 54: 22-33.
- REUTER, E. 1896. Über die palpen der Rhopaloceren. Acta Soc. Fennic. Helsinfors.
- SCHATZ, E. & J. RÖBER. 1892. Die Familien und Gattungen der Tagfalter, in Staudinger, O. & E. Schatz, Exotische Schmetterlinge, 2.
- SEITZ, A. 1921. Macrolepidoptera of the World. Vol. 5. Stuttgart.
- STANDLEY, P. C. 1922. Trees and shrubs of Mexico (Fagaceae-Fabaceae). Contrib. U.S. Natl. Herb. 23, Part 2. 296 p.
- YOUNG, A. M. 1972. The ecology and ethology of the tropical nymphaline butterfly, *Victorina epaphus*. I. Life cycle and natural history. J. Lepid. Soc. 26: 155-170.
- YOUNG, A. M. & A. MUYSHONDT. 1973. Ecological studies of the butterfly *Victorina steleneis* (Lepidoptera-Nymphalidae) in Costa Rica and El Salvador. Stud. Neotrop. Fauna 8: 155-176.