Geographic Variation of the Hidden Wing-Pattern and the Subspecies of Gonepteryx rhamni (L.) in Europe and Asia Minor (Lepidoptera, Pieridae)¹

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With 16 figures and 1 map

One of the most remarkable features of *Gonepteryx* Leach, a butterfly genus endemic in the Old World, is the presence of two widely separated centres of specific diversity, inhabitants of which show close cladistic relationships. One of these centres – the Western – is in central and southern Europa and along the shore of the Mediterranean; the other – the Eastern – is within the area of the great mountains of South-East Asia and the littoral area of the Pacific Ocean.

Each of these centres is characterized by specific endemic forms, most of which are of strictly local occurence. Only one species, *Gonepteryx rhamni* (L.), is of widespread occurence – it inhabits nearly the entire area of the Palaearctic region, with the exception of the extreme north-eastern parts of Asia, where, along the Okhotsk sea shore, it does not cross the limit of latitute 60° northwards; it is also absent from Kamchatka. It is found throughout Europe.

A study of evolution in the genus *Gonepteryx*, undertaken earlier, showed that the main tendencies in its historical development were (1) a decrease, and nearly complete disappearance, of the wing-pattern; (2) a marked reduction of the orange pigmented areas on both wings – in most species this colour remains just as small orange discal spots; (3) contraction, and nearly total elimination, of the areas that reflect ultraviolet light on the hindwings (NEKRUTENKO, 1968).

The situation of a given population relative to the above mentioned tendencies allows one to assess the degree of its evolutionary divergence from the primitive condition. This, together with palaeogeographic data, may lead to a reconstruction of the group cladogenesis and its course in space and time.

This report deals with the so-called "hidden" wing-pattern, visible on photographs taken with ultraviolet rays, of *Gonepteryx rhamni* in connection with its geographic distribution and subspecific position in Central Europe and

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Asia Minor. The two regions are considered here together, since their *Gonepteryx rhamni* are linked by common origin, so that their consideration within narrower geographic limits would be both impossible and meaningless.

Gonepteryx rhamni rhamni (Linnaeus) Fig. 1 - 4

The hidden wing-pattern of the nymotypic subspecies is characterized by the wide, dark marginal zone of the forewing; the central bright spot of the hindwing is only present in some specimens, in which case it is very small and sharply delimited. The dark marginal zone of the forewing is widest near the tornal margin.

Terra typica of this subspecies is Sweden, as Linnacus' decription is based on a specimen from this country. R. VERITY (1913) in his revision of Linnacus specimens says: "male of the northern race, small, pale yellow, discal spots to small and pale as to be nearly invisible". Data on the hidden wing-pattern are based on specimens from Sweden, Norway and Leningrad.

It is possible to state, on the basis of the available material, that the distribution of the nominal subspecies is limited within Europe by the area of Quaternary glaciation, and in any case, does not extend south of latitude 50 ° North. Those inhabiting the area south of this line are of different pattern (especially in the territory of the Ukraine).

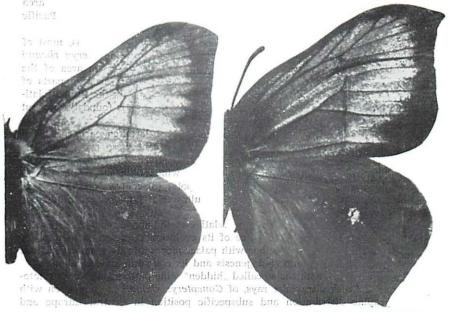


Fig. 1. Gonepteryx rhamni rhamni (L.), Lek- Fig. 2. G. rhamni rhamni (L.), Christiansund, sand, Dalarne, Sweden 147. VIII. 1945; L. BO Tomber Norgia (coll., Zool., Sammlg. München) LANDER leg. (ex coll. G. Christensen)

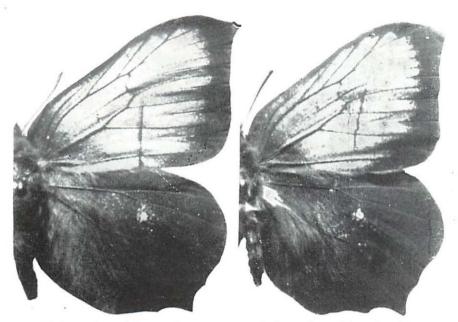


Fig. 3. G. rhanni rhanni (L.), Gammel Gronholt, Vang. Nord Sjaelland, Denmark 30. VII. 1944, G. CHRISTENSEN leg.

Fig. 4. G. rhamni rhamni (L.) — rhamni transiens Vty., München, Seeshaupt, 11. VIII. 1966, J. MOUCHA leg.

Gonepteryx rhamni meridionalis Röber Fig. 11

The hidden wing-pattern is characterized by the very narrow dark marginal zone of the forewing; this zone is widest in the apical area. The hindwing, in contrast with the nominal subspecies, bears a large central bright field which includes the entire surface of the central cell and about one third of the cubital and radial veins.

This subspecies inhabits the southernmost part of the specific range, extending into North Africa. Along the Mediterranean shore it reaches the southwestern part of Asia Minor. To the south of the Balkan peninsula it is replaced by *G. rhamni transiens* Vty. The ssp. *meridionalis* has also been recorded from Sicily (specimen from Zoologische Sammlung des Bayerischen Staates, München). In Asia Minor it probably occurs in littoral areas only, as specimens from further inland do not differ from *transiens*.

Gonepteryx rhamni transiens Verity Fig. 8 - 10

As its name implies, and this was stated by R. VERITY (1913) in his description, this form is transitional between *rhamni rhamni* and *rhamni meridio-nalis*. This transitionality is expressed not only in morphological peculiarities,

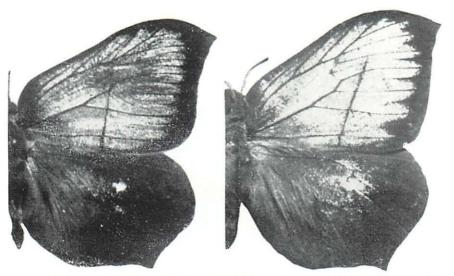


Fig. 5.—6. G. rhanni rhanni (L.) — rhanni transiens Vty., Transcarpathia, Mukatchevo circ., Forel, 22. VII. 1963, Y. KOSTYUK leg.

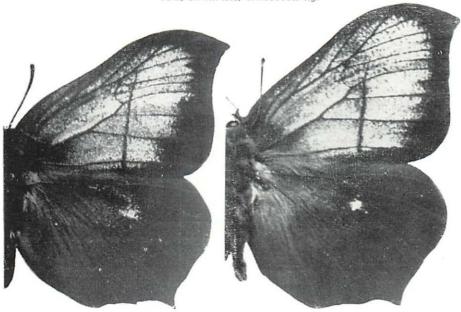


Fig. 7. G. rhamni rhamni (L.) — rhamni transiens Vty., Germania sept., Hase Gebiet, Quakenbrück u. Umg. VII. 1957, G. HESSELBARTH leg.

Fig. 8. G. rhamni transiens Vty., Italia, Liguria, Sestri Levante, 500—600 m, 12. VII. 1958. G. HESSELBARTH leg.

but also in geographic distribution. This subspecies covers the entire area of Central Europe, and is thus worthy of more detailed description.

The hidden wing-pattern is very similar to that in the nominal subspecies, with which it is connected by gradual transitions (figs. 4–7). Only when a long series is under consideration does it become possible to note that *transiens* differs from *rhamni* by the narrower dark marginal zone of the forewing and by a larger bright central spot on the hindwing, which is often surrounded by a number of bright points. In some specimens these points fuse with each other and with the central spot, producing a central spot with diffuse margins. It is noteworthy that specimens with such an enlarged spot on the hindwing are much commoner in mountainous areas. In the Ukraine they are known from the Carpathians (coll. Y. A. KOSTYUK). To a lesser degree such characters are found in specimens from places with a hot any dry summer, especially in the Steppes (Vinnitsa, Rostov-Don etc.). One might deduce from their primitive characters that they are probably relict forms that remained in the most stable environments.

The wide-scale study carried out by the auther showes that the range of this subspecies is not limited to the south of Europe. It occupies a far larger area, and its northern limit is about latitude 50° north. Eastwards this subspecies undoubtedly extends as far as the Ural Mountains.

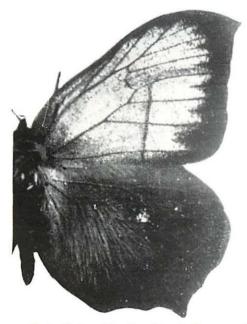


Fig. 9. G. rhamni transiens Vty., Gallia mer. Pyrenees or., Carol, 1400 m, 10. VII. 1960, G. HESSELBARTH leg.

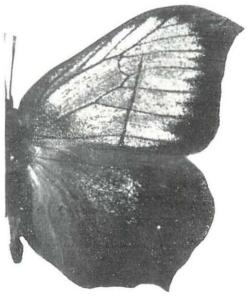


Fig. 10. G. rhanni transiens Vty., Hispania Catalonia, Monteserrat, 500 m, 9. VII. 1960, G. HESSELBARTH leg.

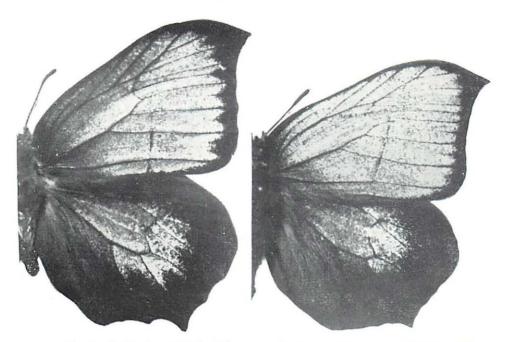


Fig. 11. G. rhamni meridionalis Röb., Marocco, Mittl. Atlas Ms., Forêt de Jaba, 1500 m. 18. VII. 1963, G. HESSELBARTH leg.

Fig. 12. G. rhamni miljanowskii Nekr., (holotypus) (coll. Zool. Mus. Kiev State University) Suchumi, W. Caucasus, 4. VIII. 1963, Y. NE-KRUTENKO leg.

Gonepteryx rhamni miljanowskii Nekrutenko

Fig. 12, 14

In visible light the colour and pattern of this subspecies does not differ from the central European forms. In ultraviolet light it differs in the following characters: the dark marginal zone of the forewing is narrow, being half of the width of that in the central European specimens; the hindwing bears a large central bright field, similar in size to that in *meridionalis*. One of the key characters that distinguishes this subspecies from the others is the absence of an incision in the hindwing.

The geographic distribution of this subspecies has not yet been fully determined, but it is possible to state that its range is smaller than that of any other subspecies, or of any other species of the genus. A serial study of specimens, collected in the area of the Soviet Union, shows that within the country the distribution of this subspecies is limited to the Black Sea coast of the Caucasus, and to the east it does not go further than Tbilisi (Georgia). Specimens from Tbilisi and Lagodekhi (coll. E. DIDMANIDZE) are transitional in character between miljanowskii and transiens. The same transitional nature

is found in specimens from Zakataly and Kodzhori (coll. Zoological Institute, Leningrad); specimens with a label "Adzhi-Kent" (coll. Zoological Museum, Kiev State University) were determined by L. SHELJUZHKO as transiens Vty. This determination is fully supported by study of their hidden patterns. Thus, the eastern limit of the range of this subspecies lies in the Tiblisi region. The northern limit extends along the main Caucasus ridge (Caucasioni), northwards of which flies the real transiens. The north-western limit is in the suburbs of Sotchi, where both milianowskii and transiens occur in equal numbers, together with intermediate forms. With a long enough series from this locality, one can detect a gradual transition between these two subspecies. The southern limit of the range of ssp. mijjanowskii is not yet known positively because of the lack of material from Turkey, especially from the Black Sea shore. Specimens in the Zoologisches Museum, Humboldt-Universität zu Berlin, labelled "Amasia" and "Pontus" are determinable as transiens. With the aid of ultraviolet photography the same determination was made for specimens from Aksehir and Baglun (Turkey) (coll. G. HESSELBARTH). Material from the British Museum (Natural History) showed that in Yozgat there is a form that does not differ from ssp. miljanowskii (fig. 14). This subspecies is also found in the Taurus Mountains (com. fig. 13). The previously mentioned



Fig. 13. G. rhamni meridionalis Röb. — rhanni miljancwskii Nekr., Taurus Mts., Turkey in Asia (coll. Brit. Mus. [N. H.])

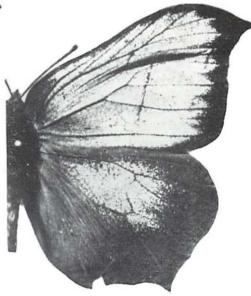


Fig. 14. G. rhanni miljanowskii Nekr., Asia Minor, Yozgat, VI.—VII. 1918, W. PHILIPS leg. (coll. Brit. Mus. (N. H.))

specimen from Sicily is rather more transitional in nature between this and meridionalis, than pure meridionalis.

All data given here were taken into account in compiling the distribution scheme of the subspecies of *Gonepteryx rhamni* in the western Palaearctic (see map).

In reconstructing the phylogenetic relationships of the species and subspecies of the genus, I suggested that those belonging to the subgenus Isogonepteryx are more primitive in character than the others. Isogenepteryx is a well differentiated, compact group, uniform in its morphological characters and geographical distribution. In all of them is found the well developed orange pigmentation and the special structure of the genital armature, especially the uncus. The hidden wing-pattern peculiarity is the narrowing of all dark elements, and the presence on the hindwing of a large bright central field. (fig. 15, 16). Representatives of Isogonepteryx (cleopatra [L.], cleobule Hübn., maderensis [Feld.]), inhabit the narrow area which includes the Mediterranean region and some islands in the Atlantic Ocean (the Canaries). This area is considered as an Oikumena, whence in the geological past the ancestors of recent Brimstones have spread. Most probably is took place within the pre-Neogene era. This suggestion is supported by the etablished general tempo of evolution in the Lepidoptera (ZEUNER, 1943, 1960; NEKRUTENKO,

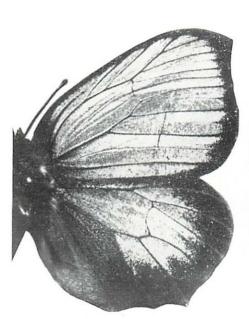


Fig. 15. G. cleopatra (L.), Dalmatia (coll. LEECH in coll. Brit. Mus. [N. H.])

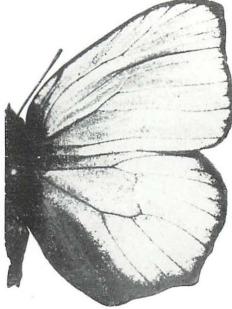


Fig. 16. G. maderensis (Feld.), Madeira, Wollaston, 2000 ft. (coll. Brit. Mus. [N. H.])



Map 1. Distributional pattern of Gonepteryx rhamni (L.) subspecies in the West Palaearctic

1966), and the fact that at this time environmental conditions in the entire area of the recent Palaearctic were homogeneous, so that insects could scatter from their centres of origin.

The greatest similarity to *Isogenepteryx* appears to be found in the North African *meridionalis*, especially in its hidden wing-pattern. *Meridionalis* is connected with the nominal subspecies via *transiens*. The large central bright field of *meridionalis* is the very character that links *Isogonepteryx* with *rhamni* (which belongs to the subgenus *Gonepteryx* s. str.). This bright field shows progressive reduction in a South-North direction.

As for the position in this complex of ssp. *miljanowskii*, it seems to be a relic, remaining in the Black Sea area from the times when bright-field-bearing ancestors inhabited the entire Ponto-Caspian area. The relict nature of this subspecies is also supported by its narrow range, by the homogenity of environmental conditions within the entire area of its occourence, and by the strong geographical barriers along the limits of its range. It is possible to make the assumption that, after the full decline of orange pigment in the ancestors of *G. rhamni*, they retained the large bright spot on the hindwing, which was positively correlated with orange colour, and in this respect were

closer to the original forms (and to recent *Isogonepteryx*). Nowadays this character has only persisted in populations inhabiting areas with a decidedly maritime climate (for example, eastern *rhamni amurensis Graes., amintha formosana* Fruhst. etc.). This provides additional evidence that the origins of the group unter consideration had its place on the shores of a great basin. The presence of such primitive forms in the Mediterranean area shows that such a basin was the very same Mediterranean Sea, or the waters that extended over that area.

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Summary

The paper presents descriptions of four subspecies of Gonepteryx rhamni (L.) with special attention to the hidden wing-pattern, visible on photographs taken with ultraviolet light. Geographic occurence for each of these subspecies considered and some evolutionary suggestions are given.

NOTE: As it was recently established by this author, British *G. rhanmi* population seems to belong to another subspecies, different from continental form and, on other hand, from ssp. *gravesi* Huggins of Ireland. This subject is to be considered later on.

Zusammenfassung

Geographische Variation des Hinterflügel-Musters und die Unterarten von Gonepteryx rhamni (L.) in Europa und Kleinasien.

Vier Unterarten von Gonepteryx rhanni (L.) werden unter besonderer Berücksichtigung der Zeichnungsmuster der Hinterflügel beschrieben, die in Ultraviolett-Aufnahmen sichtbar sind. Die geographische Verbreitung der Unterarten und Vorstellungen über ihre Entwicklungsgeschichte werden besprochen.

Bemerkung: Nach neueren Feststellungen des Autors scheinen britische Populationen von G. rhammi zu einer anderen Unterart zu gehören, die sich sowohl von den Kontinentalformen als auch von der ssp. gravesi Huggins in Irland unterscheidet. Hierüber wird später berichtet.

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