SYSTEMATICS AND EVOLUTION OF THE
Palaearctic Spialia Species (Lepidoptera,
Hesperiidae)

by

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Abstract

The Palaearctic members of Spialia have been revised taxonomically. Two species groups have been distinguished, viz. the phlomidis group and the sertorius group. The former comprises the species phlomidis, osthelderi, geron and doris, and is related to the African species spio. The sertorius group has two Palaearctic members, viz. sertorius and orbifer, united in a superspecies, and two members outside the Palaearctic, viz. the African mafa and the Indian galba.

By analyzing some characters as to their plesiomorphous or apomorphous conditions, a reconstruction has been made of the evolutionary and geographic history of the two species groups. This reconstruction forms the theoretical basis for the arrangement of the species and subspecies adopted.

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1. INTRODUCTION

1. a. General

The aim of this study is to examine the phylogenetic relationships of the Palearctic members of the genus *Spialia* by means of a reconstruction of the evolutionary and geographic history. For this purpose the species concerned have been revised taxonomically and several characters have been analyzed as to their conditions being derived or primitive. This leads to an arrangement of the species supposedly reflecting the phylogenetic relationships. This arrangement is not very different from former arrangements, but especially in *sertorius* and its allies the solution of the perpetual problem "species or subspecies?" is somewhat different from all former solutions. This is mainly due to the subspecies concept.

Under the term "subspecies" usually a number of various types of geographic variation is described. This fact appears to be little recognized and virtually is a source of much confusion. Some authors apply the term "subspecies" to any recognizable population, others use the term to denote rather arbitrary parts of the geographic variation. Recently, Dobzhansky (1970) defined a subspecies as "a race that a taxonomist regards as sufficiently different from other races to bestow upon it a Latin name". To my opinion such a concept must lead to confusion. This is not the place for an exhaustive discussion on the subspecies concept, therefore I will only stress that for a student wishing to trace the geographic history of a species, only that part of the geographic variation is useful for him which arose by geographic isolation. Consequently, in my paper on the genus *Pyrgus* (De Jong, 1972) I presented the following definition:

A subspecies is an, at present or formerly, geographically isolated group of populations of a species, which can be distinguished by one or more characters from other such groups of populations of the species.

The fact that the existence of a former geographic isolation must remain hypothetical cannot be a serious objection, so long we do not use the subspecies thus defined for proving the former existence of such an isolation. Virtually the distinction of subspecies is a hypothesis about the geographic history of the species. The hypothesis may be wrong, but the meaning is clear. I cannot see the use of a subspecies that is an aggregate of various kinds of variation. Some people may object that we better stick to the facts, but what is the use of facts we do not use?

The remainder of the geographic variation lays in the field of the ecologist and geneticist, rather than in that of the zoogeographer. However, the last-named is in the best position to notice this variation. Without experiments it is difficult to ascertain whether a variation is hereditary or not. Nevertheless, I have attempted to distinguish between non-genetic and genetic variation, which I have termed ecophenotypic and clinal, respectively. I consider it senseless to use a trinomen in the case of clinal variation. It not only would cause confusion with subspecific distinctions, but it also would suggest discontinuities where there are only continuities. It seems better to describe clinal variation than to denominate it. In many cases, however, parts of the clinal variation have already been described as subspecies. In such cases I am using Latin names, but separately and not as a trinomen.

The same applies to ecophenotypic variation. A large part of the nomenclatural and taxonomic confusion, at least in butterflies, is due to the practice of describing ecopheno-
typic varieties as subspecies (e.g. the form *hibiscæ* of *sertorius*, see chapter 4).

b. Wing markings and genitalia

For the wing markings and genitalia I may refer to my paper on *Pyrgus* (De Jong, 1972). However, some parts of the male genitalia of *Spialia* are not so highly differentiated as in Palaearctic *Pyrgus* species. Therefore, the names of the parts can more easily be brought into accordance with the more currently used names as expressed in Tuxen (1970). So, with regard to the names used in *Pyrgus* the following alterations are made in this paper:

1. lateral apophyses become gnathos. In *Spialia* this structure is much simpler than in *Pyrgus*.

2. harpe becomes costa. In *Pyrgus* the distal end of the dorsal part of the valve is highly differentiated. Also in *Spialia* this part is differentiated, but in a different way and presumably by an independent evolution. It seems advisable to term this structure in *Spialia* by a trivial name and I use the name costal process. It would be senseless to replace the terms style, stylifer and antistyle in *Pyrgus* also by costal process.

3. cuiller becomes cucullus. Also in *Pyrgus* it may be advisable to introduce this alteration.

c. Acknowledgements

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d. Methods and measurements

All names given to species, subspecies and forms of *Spialia* in the Palaearctic have been included in this study, with the exception of the few names relating to individual varieties. A full account of these names can be found in Evans (1949).

To avoid confusion between species and subspecies in the text, a species is indicated by the combinations *Spialia a-n*, *S. a-n*, or simply *a-n*, a subspecies by the combination *a-n b-n* or by ssp. *b-n*. Names referring to the infrasubspecific variation can be recognized by the word “forma” preceding the name of the variety.

Measurements refer to the length of the fore wing from base to apex.
2. Delimitation and classification of the genus *Spialia*

The genus *Spialia* was erected by Swinhoe (1913 : 99) to include the species *galba* (type-species), *zebra*, *geron* and *sao* which were previously placed in the collective genus of "black and white Skippers" known under the names *Hesperia* and *Syrichtus*. Thus, Swinhoe only included species occurring within the boundaries of the former British India. Evans (1937) placed also the Ethiopian black and white Skippers in *Spialia*. This extension of the genus is generally accepted, also in this study.

As a revision of the generic divisions of the *Pyrgus* group (Evans, 1949) is intended in the near future, it may suffice now to mention only the most conspicuous characters of *Spialia*, as against the genera *Pyrgus* and *Muschampia* (sensu Evans; recte *Syrichtus*). The fact that the last named genus is heterogeneous does not need to bother us here.

From *Pyrgus* species those of *Spialia* can easily be distinguished by the presence of a more or less well-marked and complete series of submarginal spots on the fore wing upperside and by the place of the median spots in spaces 4 and 5 (if present) that are in line with the median spots in spaces 6 to 8. In *Pyrgus* the submarginal spots are incomplete and faint or absent and the median spots in 4 and 5 (usually present and distinct), are not contiguous to the spots in 6 to 8, but much nearer the termen.

Other distinguishing characters can be found in the males, viz., a costal fold in the fore wing and a hair tuft on the hind tibiae, fitting into a thoracic pouch in *Pyrgus*. Both these secondary sexual characters are absent in *Spialia*, only the males of some Ethiopian species have an indistinct costal fold.

From *Syrichtus* species *Spialia* species can be distinguished by the median spot in space 2 of the fore wing upperside which is central between the cell spot and the median spot in space 3 or nearer the latter. In *Syrichtus* species the median spot in 2 is nearer to the cell spot than to the median spot in 3. Moreover, the termen of the hind wing is more or less crenulate in various *Syrichtus* species, but never so in those of *Spialia*. The males of *Syrichtus* species usually have a costal fold.

Few authors have tried to subdivide the genus *Spialia*. Warren (1926), while dealing with Palearctic species (under the name *Powellia* Tutt, a junior homonym of *Powellia* Maskell, 1879; see Verity, 1940), distinguished two species groups, viz. the *geron* group and the *sертorius* group. I disagree with Warren about the assignment of species to these groups.

Picard (1947) proposed a more radical subdivision by erecting a new genus, viz. *Platygnathia* for *phlomidis*, *geron* and *doris*. However, he did not study the Ethiopian species and therefore, his classification is somewhat premature. For a revisional study of the taxonomy of the genus which I hope to complete in the near future, I have studied the male genitalia of all Ethiopian *Spialia* species. As a result of this study I consider the species *spio* a link between the relatives of *phlomidis* and the Ethiopian species. The genus may be subdivided into species groups, but there is no apparent use in making genera of such groups. I am an opponent of the use of subgenera: their application does not solve problems, but only adds to nomenclatural difficulties. Therefore I propose to subdivide the genus *Spialia* only into species groups, while placing *Platygnathia* as a junior subjective synonym of *Spialia*.

In the Palearctic two species groups can be distinguished:

(1) the *phlomidis* species group, including the species *phlomidis*, *geron*, *osthelderi* and *doris*. 
Male genitalia (Fig. 1—8). — Aedeagus with a strongly sclerotized and indented crest, latero-ventral in the middle, or a long, unindented branch in the same place, and with an extended apex. Cucullus spined at apex. Costa spined on dorsal surface and at the ventro-distal end, or only at the ventro-distal end.

Female genitalia (Fig. 9—13). — Two heavily sclerotized and indented wing-like structures at the base of the eighth sternite. No distinct genital plate.

External characters. — On the upperside of the fore wing a conspicuous spot or bai at the end of the cell.
Fig. 9—11. Female genitalia of Spialia. 9, S. phlomidis phlomidis (Greece), ventral side; 10, idem, seen from the left; 11, S. geron geron (Baluchistan, Kahan), ventral side.

(2) the sertorius species group, including the species sertorius and orbifer (united into a superspecies). Two non-Palaearctic Spialia species can also be referred to this group, viz. the Oriental galba and the Ethiopian mafa.

Male genitalia (Fig. 24—35). — Aedeagus without crest or branch and apex not extended. Cucullus little differentiated, without spines. Costa at ventro-distal end with a more or less ellipsoid extension bearing long upcurved spines. Between costa and cucullus a densely haired fold at the inside of the valva.

Female genitalia (Fig. 21—23). — No wing-like structures. In Palaearctic species genital plate narrow in proximal half, well developed.

External characters. — On the upperside of the fore wing, spot at end of cell faint or absent in Palaearctic species; galba can be distinguished from the phlomidis group by the inner spot in space 7 of the hind wing underside being placed directly over the basal spot in the cell; mafa has a pale basal spot in space lc of the hind wing underside, which is absent in the phlomidis group.
3. The *phlomidis* species group

The species of the *phlomidis* group can be regarded as closely related and Evans (1956: 750) is correct in stating that they "looked at from a very broad point of view, might be treated as conspecific". As a great overlap exists in the distributional areas of the species, it is undesirable to unite them even into a superspecies, but by bringing them together into a species group we can indicate their supposedly close relationship.

The species can be distinguished as follows.

Key to the species of the *phlomidis* group

1. Central band of hind wing underside directed and more or less conjoined to inner spot in space 7 (Fig. 18). Costa of valva without spines dorsally (Fig. 1). Aedeagus with a sclerotized crest medially (Fig. 2). Papillae anales (Fig. 14) rather pointed,
basal lobe large, covering about three quarters of base; length ratio papilla : apophysis posterior, 5 : 9  

Central band of hind wing underside not conjoined to inner spot in space 7, but directed more or less to apex. Costa of valva with spines dorsally. Aedeagus with a sclerotized crest or branch medially. Papillae anaes bluntly rounded, basal lobe covering half of base or less, apophyses posteriores relatively shorter  2

2. Central band of hind wing underside more or less directed to outer spot in space 7, without touching it (Fig. 20). Discal spot in space lb of fore wing undersides not touching vein 1. Small, $\delta$ 8.6—12.4 mm. Costa of valva distally strongly concave and reaching beyond cucullus (Fig. 7). Aedeagus with a sclerotized crest medially (Fig. 8). Basal lobe of papillae anaes (Fig. 17), a small flap, nearly circular; length ratio papilla : apophysis posterior, 5 : 7.5  

Central band of hind wing underside directed to a point between the inner and outer spots in space 7 (Fig. 19). Discal spot in space lb of fore wing undersides usually touching vein 1. Costa of valva not extending beyond cucullus. Basal lobe of papillae anaes elongate. Larger, $\delta$ 11—14.2 mm.  3

3. Colour of hind wing underside greenish. Spot at base of cell of fore wing undersides and cell spot of hind wing undersides present, or if absent, then colour of hind wing underside whitish with faint markings. $\delta$ 11—13.6 mm. Costa of valva strongly curved (Fig. 6). Aedeagus with a crest medially. Papillae anaes with short apophyses posteriores; length ratio papilla : apophysis posterior, 5 : 5—6; basal lobe broad
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osthelderi

- Colour of hind wing underside yellowish. Basal cell spots of fore and hind wing uppersides usually absent. 11.7—14.2 mm. Costa of valva more gently curved (Fig. 4)*. Aedeagus with a branch medially (Fig. 5). Papillae anales (Fig. 15) with slightly longer apophyses posteriores, length ratio papilla : apophysis posterior, 5 : 7, basal lobe narrower.

geron

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Fig. 18—20. Underside of left hind wing of Spialia. 18, S. phlomidis phlomidis (Greece); 19, S. osthelderi gecko (Semnan); 20, S. doris evanida (Karachi)

Note. The differences in the female genitalia are much less conspicuous than in those of the male. It is recommendable to examine the papillae anales freely floating in water or alcohol, as their shape is easily influenced by the pressure of a cover glass.

There are also differences in the sclerotization of the postvaginal region. This is evenly sclerotized in phlomidis, with a central narrow membranous gap in osthelderi and doris, and with a wide central membranous region in geron.

The strongest sclerotization of the wing-like structures was found in osthelderi and the weakest in doris. However, this may be partly due to differences in mounting (e.g. length of maceration by KOH).

Spialia phlomidis (Herrich-Schäffer)

Distribution (Map 1). — From Macedonia and Albania through Greece and Turkey to NE Iran. A local species, known only from the following localities:
- Albania: Kula e Lumes, Maliqsee, Korce (Alberti, 1965; material examined);
- Yugoslavian Macedonia: Orasje, Drenovo, Ohrid, Petrina planina (Thurner, 1964; material examined);
- Greece: Morea (Rebel, 1902); further only “Greece” (Oberthür, 1912; material examined);
- Turkey: Brussa, Amasia, Tokat, Goynucek, Ayac Dagi, Berud Dagh (Taurus), “Armenia” (Staudinger, 1881; Oberthür, 1912; material examined);
- South Russia: “S. Russia”, “Caucasus”, Kasikaporan, Ordubad (material examined);
- Iran: Shahrud, “Hyrcania” (material examined);
- Syria: Akbès (Oberthür, 1912);
- Lebanon: Bludan (Ellison & Wiltshire, 1939), Mt. Hermon (material examined).

*) The figure of the valva of geron by Reverdin (1914) represents that of osthelderi!
Groum-Grshimailo (1890) recorded this species from Pamir, but this observation probably concerns *osthelderi gecko* or *geron struwei*.

Habitat. — According to Thurner (1964) in Macedonia mainly at low altitudes, exceptionally up to 1600 m; in Turkey to 1300 m (Ayac Dagi, material examined), at Bludan between 1700 and 2000 m (Ellison & Wiltshire, 1939). Always in dry and hot localities.

Biology. — All the known specimens are from June and July. No further records about the biology.

Geographic variation. — Two subspecies can be distinguished. The material, however, is very scanty, especially from the eastern part of the range.

**Spialia phlomidis phlomidis** (Herrich-Schäffer)

Herrich-Schäffer, 1845. — Syst. Schmett. Eur. 1 : 153; Hesp. pl. 2 fig. 8, 9. (For date of publication, see Hemming, 1937).

Type-locality: Turkey (shores of the Sea of Marmora).

Material examined. — 105 ♂ 33 ♀ : 28 ♂ 10 ♀ Macedonia (Ohrid) (HC, ML, ITZ), 21 ♂ 10 ♀ Albania (Korce) (BM), 12 ♂ 2 ♀ Greece (BM, ML), 37 ♂ 9 ♀ Turkey (Brussa, Tokat, Amasia, Goynucek, Ayac Dagi, Berud Dagh, "Pontus", "Turkey") (BM, ML), 1 ♂ 1 ♀ Kasikaporan, 2 ♂ Caucasus, 2 ♀ S. Russia, 1 ♂ Ordubad, 1 ♂ 1 ♀ Iran (Shahrud, "Hycania") (all BM).

Distribution. — As that of the species, except Anti-Lebanon and Mt. Hermon.

Subspecific characters. — ♂ 13.2—15.7 mm. A large and strongly marked form, if compared with ssp. *hermona*.

Variation. — Hemming (1932a) compared a long series of freshly emerged specimens (mainly males) from Mt. Chelmos and two specimens from Parnassos with specimens from E. Turkey, Armenia and Iran. He found differences, the specimens from the eastern part of the range being slightly larger, greyer and with larger spots. On account of this difference he described a new subspecies, viz. *phlomidis eupator* (type-locality: Amasia),
occurring in the eastern part of the range of *phlomidis*, while *phlomidis phlomidis* flies in the Balkans and in the western part of Asiatic Turkey (e.g. at Brussa).

I could examine much more material from the Balkans than Hemming. This material does not support the separation made by Hemming. Although the holotype and allotype of *phlomidis eupator* (in the BM) agree very well with the description, they are not representative for the eastern populations, as far as can be judged from the limited number of specimens available. We have to wait for further material from the eastern part of the range of *phlomidis* before we can hope to make a subspecific separation.

**Spialia phlomidis hermona Evans**


Type-locality: Mt. Hermon.

Material examined. — 1 ♂ Mt. Hermon, 30.VII.1945 (holotype) (BM).

Distribution. — Only the type specimen is known, but Ellison & Wiltshire (1939) recorded the occurrence of a small *phlomidis* near Bludan in the Anti-Lebanon, that undoubtedly concerns this subspecies.

Subspecific characters. — According to Evans (1956) this subspecies is smaller than *phlomidis phlomidis*, ♂ 12 mm, and on the upperside exactly like *osthelderi* gecko, but the valva resembles *phlomidis phlomidis*. To this I can only add that the fringes seem to be somewhat narrower relatively than in *phlomidis phlomidis* and that I was not able to find an essential difference in the male genitalia.

**Spialia osthelderi (Pfeiffer)**

Distribution (Map 2). — From SE. Turkey to Central Asia, but only few localities are known:

*Turkey*: Marash, Diarbekr (Pfeiffer, 1932; material examined); Sivrice (De Lattin, 1950); Yüksel Dagh (Amanus Mts) (material examined).

*Syria*: Akbès (material examined).

*Lebanon*: Bscherre (material examined).

*Iraq*: Kizil-Robat, Mirjana, Suleimanyeh (material examined).

*Iran*:“Hyrcania”, Shahrud, Keredj, Semnan, Mashad, Seguck near Kerman (material examined); Shiraz, Sine-Sefid, Tchouroum (Brandt, 1939; material examined).

*Afghanistan*: Reschke (material examined; I was not able to trace this locality, possibly this is not the name of a locality but of a collector). Evans (1949) recorded 2 ♂ 1 ♀ from Kabul; these specimens, however, proved to belong to *geron*.

*C. Asia*: Ketmen Tjube (Sussamyr Mts) (material examined).

Habitat. — According to Pfeiffer (1932) flying on slopes up to 1000 m; in SW Iran up to 2600 m (material examined); in Iraq desert foothills and lower middle heights of the mountains (Wiltshire, 1957).

Biology. — According to Pfeiffer (1939) two generations per year. The specimens examined have been collected in all months from April till July and in September.

Geographic variation. — Evans (1949) distinguished two subspecies as follows:

(1) **ssp. osthelderi** — Above markings reduced, particularly on the hind wing upper-
side, where the discal spot in space lc and the basal cell spot are absent usually. Hind wing underside almost all white, with all markings faint.

(2) ssp. gecko — Above and below with well-marked spots. On the upperside of the fore wing basal cell spot present, as also the cell spot on the hind wing upperside.

This suggests a clear-cut difference between the two subspecies, but the impression is wrong. The only difference upon the upperside I could establish concerns the discal spot in space lb of the hind wing which is always visible and sometimes large in ssp. gecko, mostly inconspicuous or absent, but sometimes also large (e.g. ♂ paratype), in ssp. osthelderi.

Also on the underside of the hind wing the difference is not clear-cut. In ssp. osthelderi the ground colour is always whitish, so that the white markings are very faint. In ssp. gecko the ground colour is olive greenish or brownish with well-marked spots, but in two males from the vicinity of Shiraz (Cornée, 2600 m; Sine-Sefid, 2200 m) the ground colour is whitish and the markings faint, so that these specimens are indistinguishable from ssp. osthelderi.

As the material is so scanty, the overlap of differentiating characters needs not be significant, but it can also mean that there is a large transitional zone or a clinal variation in the character mentioned. For the time being it seems advisable to consider both forms separate subspecies. The white underside of the hind wing does not appear to be a character of a purely ecological nature, forming a part of a cline. It is interesting to note that this character also occurs in the two Hesperid species Pyrgus meloitis meloitis Duponchel (see De Jong, 1972) and Syricbtus tessellum nomas Lederer (see Warren, 1926), both occurring in Turkey and Syria, much like osthelderi osthelderi.

Spialia osthelderi osthelderi (Pfeiffer)


Type-locality: Marash (Turkey).

Material examined. — 9 ♂ 6 ♀ : 4 ♂ 2 ♀ Marash (3 ♂ 2 ♀ paratypes) (ZSM, BM), 1 ♂ Diarbekr, 1 ♂ Amanus (Yükeş Dagh), 1 ♂ Bscherre (Lebanon) (all ZSM), 1 ♀ Akbès, 1 ♂ 3 ♀ River Dyala (Kizil-Robat, Mirjana), 1 ♂ Suleimanyeh (Kurdistan) (all BM).

Subspecific characters. — See above. ♂ 11.5—13.6 mm. Small specimens possibly belong to a second generation.

Distribution. — The western part of the range, eastward probably to W. Iran.

Spialia osthelderi gecko Evans


Type-locality: Hyrcania.

Nomenclature. — Pfeiffer (1939) mentioned a new form of osthelderi that he would name and describe before long. Shortly thereafter, in a list of butterflies from S. Iran, Brandt (1939) mentioned "Spialia osthelderi struveoides Pfeiffer". This is undoubtedly the same form as gecko, since gecko looks somewhat like Spialia geron struvei (at least, if compared with osthelderi). As the name struveoides was published in 1939, gecko would fall as a junior subjective synonym. However, Dr. Forster kindly informed me
that Pfeiffer never published the name *struveoides*. As the name is mentioned by Brandt without a description, it is not available in nomenclatural sense.

Material examined. — 15 ♂ 5 ♀ : 4 ♂ 1 ♀ Hyrcania (1 ♂ holotype) (BM), 1 ♂ Semnan (MW), 1 ♂ Mashad (WLB), 3 ♂ Keredj, 5 ♂ 1 ♀ Fars (Shiraz, Sine Sefid, Tchouroum, Comète) (all ZSM), 1 ♂ Shahrud, 1 ♀ Seguck near Kerman, 1 ♀ Afghanistan (Reschke), 1 ♀ Ketmen Tjube (Sussamyr Mts) (all BM).

Distribution. — The eastern part of the range, from Iran to C. Asia.

Subspecific characters. — See above. ♂ 11—13.6 mm. Small specimens may belong to a second generation.
Spialia geron (Watson)

Distribution (Map 3). — From Ordubad (Russian-Iranian frontier, west of the Caspian Sea) to Barkul and Hami (eastern end of Tian Shan), but extremely local and only known from the following localities:

Iran: Ordubad (Evans, 1949: "Ordub") (material examined).
Afghanistan: Arbarp (10 mls W. of Kabul) (material examined; wrongly identified as osthelderi by Evans, 1949).
W. Pakistan: Baluchistan (Quetta and surroundings) (Watson, 1893; material examined).
C. Asia: "Ferghana" (material examined); Issyk Kul, Barkul (Püngeler, 1914); Dsharkent (= Panfilov) (Pfeiffer, 1932; material examined); Hami (material examined).

The Pyrgus phlomidis recorded by Groum GrshimaIio (1890) from Pamir, probably is the present species, or osthelderi gecko. Clench & Shoumatoff (1956) listed a badly worn female from Panjao, southwest of Koh-i-Baba (Afghanistan) as a possible geron. This identification may be correct, but the specimen may also belong to osthelderi gecko.

Habitat. — Not recorded.

Biology. — Presumably two generations per year. The specimens from Baluchistan in the BM date from the periods February to March, and May to September, respectively.

Geographic variation. — The specimens from Afghanistan and Baluchistan differ constantly in size and in the male genitalia dissected: ten males from Afghanistan and Baluchistan, four males from Ferghana and one male from Ordubad.

Spialia geron geron (Watson)

Type-locality: Quetta (Baluchistan).

Material examined. — 42 ♀ 20 ♂ : 2 ♂ 3 ♀ Arbarp (Afghanistan, 10 miles W. of Kabul), 40 ♂ 17 ♀ Baluchistan (Quetta, Urak, Old Urak, Kahan, Chotair, Pasni Rek, Gunduk, Bolan, Giridik; 1 ♂ type Quetta) (all BM).

Distribution. — Only known from Afghanistan and W. Pakistan.
Subspecific characters. — ♂ 11.7—13.5 (—14) mm. Male genitalia (Fig. 4, 5): apex of cucullus much more pointed than in ssp. struvei, overlapping a great part of the costa; dorsal surface of costa densely clothed with small spines, but coarser than in ssp. struvei; ventro-distal end of costa unspined.

It is interesting to note that Reverdin, who, after Rambur, was the first to put the chaos of the Hesperiidae in order, perhaps never saw a true geron. His sketch (1914) of the valva of geron clearly shows an osthelderi, a species that was described eighteen years later. Perhaps the same applies to Warren (1926, Pl. 6 Fig. 5), but his photograph is to dark to be decisive.

Spialia geron struvei Püngeler

Püngeler, 1914. — Iris 28 : 37, pl. 2 fig. 13, 20.
Type-locality: Barkul.
Material examined. — 6♂ 3♀ : 1♂ Ordubad, 4♂ 2♀ Ferghana (BM), 1♂ Dsharkent, 1♀ Hami (ZSM).

Distribution. — The few known localities of this species outside Afghanistan and Baluchistan (see the distribution of the species).

Subspecific characters. — ♂ 13.5—14.2 mm. Male genitalia (Fig. 3): apex of cucullus not strongly developed, just reaching the costa; dorsal surface of costa densely clothed with very fine spines; ventro-distal end of costa spined.

**Spialia doris** (Walker)

Distribution (Map 4). — Widely but apparently highly discontinuously distributed from Morocco to India.

In Morocco only captured in the following localities: El Aioun du Drâa (Rungs, 1945) and High Atlas, Ziz Valley (Evans, 1949) and Ksar-es-Souk (material examined). Several localities in N. Egypt, south to Heluan (Graves, 1925; Hemming, 1932b; Evans, 1949). From Jordan only known from Qasr Azraq and Hazin (Hemming, 1932b). Widely distributed in W. and SW. Arabia, from Jidda southward, and in Africa from Port Sudan and Kordofan to Somaliland (material examined) and N. Kenya (Baringo District; specimen in National Museum, Nairobi, according to personal communication by Mr. J. H. Lourens). SW. and S. Iran (Ahwaz, Kerman), Sind, Cutch, Punjab and Rajputana (Evans, 1949; material examined). Hemming (1932b) recorded a male from River Dyala (Iraq), but this specimen (in the BM) belongs to *Spialia osthelderi*.

Habitat. — Desert, as far as the food plant grows. In Yemen up to 2800 m (material examined).

Biology. — In Egypt possibly two generations per year. The material in the BM dates from the periods March—April and September—October. Reverdin (1914), however, used for his description of *amenophis* (see below), a male caught August 1st and a male caught November 11th (both from Heliopolis). The spring and autumn forms differ.
in size.
In Arabia the species is known from all months in the period September to May, but
in summer the species seems to be absent, apart from a few specimens taken in July.
No size difference between the spring and autumn specimens could be established.

From other parts of the range the data are too scanty to allow for reliable conclusions.
The only known foodplant is *Convolvulus lanatus* (Graves, 1925: Egypt), a species
of the desert.

Geographic variation. — There is a geographic variation in the size, the colour of the
underside and the extension of the spots of the upperside.

**Spialia doris daphne Evans**

Type-locality: Ziz Valley (High Atlas).

Material examined. — 13 ♂ 5 ♀ : 1 ♂ Ziz Valley, 21.IV.1935 (holotype) (BM),
12 ♂ 5 ♀ Ksar-es-Souk, 8—18.V.1950, 3500 ft (CW, ML).

Distribution. — Only known from S. Morocco. Rungs (1945) recorded the species
from El Aioun du Drââ (S. Morocco) under the name "Pyrgus doris adenensis Butl.".
This may be *daphne*, as this subspecies shows the greatest resemblance to subspecies *doris*
(adenensis is a synonym of *doris*).

Subspecific characters. — The original description reads: "Unh very dark greenish
brown, markings sharply defined, basal cell spot elongate. Upf basal cell spot elongate,
no spots in spaces 4 and 5: outer discal spot in space 1b vestigial. ♂ F 12½ mm." This
description of the type is correct, except that the length of the fore wing is only 11.5 mm.
The other specimens, however, show some variation, viz. on the fore wing upperside
the discal spots in spaces 4 and 5 and the outer discal spot in space 1b may be present,
and the length of the fore wing varies from 11 to 12 mm.

Note. — It is a bad usage to describe subspecies on account of a single specimen.
Although it is to be expected that in a geographically isolated population differentiating
characters will develop, this is not necessary. As to the present instance, the type of ssp.
*daphne* could have been an extreme variation of a population that is otherwise similar to
ssp. *doris*, the more so as the variation concerns characters that are liable to variation
in ssp. *doris*. Fortunately, the distinction of ssp. *daphne* is not superfluous, but Evans
could not know that on account of his single specimen!

**Spialia doris amenophis** (Reverdin)

Type-locality: Heliopolis (Egypt).

Material examined. — 13 ♂ 12 ♀. Spring form: 7 ♂ 5 ♀ Mokattam Hills (near
Cairo) (BM), 1 ♂ 1 ♀ Heliopolis (BM, MW). Autumn form: 4 ♂ 5 ♀ Qassasin,
1 ♀ Wadi Rished (near Heluan), 1 ♂ Wadi el Tih (all BM).

Distribution. — Northern Egypt, from northern Sinai (Mehemdia; Graves, 1925) to
Heluan; Jordan (Qasr Azraq, Hazim; Hemming, 1932b).

Subspecific characters. — Spring form larger than autumn form: ♂ 11.1—12.4 mm
(♀ up to 13.7 mm!) and ♂ 10.2—11.2 mm, respectively. On the upperside the markings very broad. The discal spots in spaces 3 to 8 may be fused into an irregular band, while in other forms the discal spots in spaces 4 and 5 are minute or absent.

**Spialia doris doris** (Walker)

Walker, 1870. — Entomologist 5 : 56.

Type-locality: Tajora, Red Sea.

Material examined. — 58 ♂ 40 ♀: 42 ♂ 35 ♀ Arabia (Jidda, Tihama Sabata, Yemen, Aden, Hadramaut) (BM, MW), 4 ♂ Perim, 2 ♂ French Somaliland (1 ♂ Djibouti; 1 ♂ holotype, Tajora), 6 ♂ 3 ♀ Somaliland (Ghibdo River, Djibouti, Berbera, Hargeisa, Sheikh, Saleh Spring, Bihendula, Buran), 2 ♂ 1 ♀ Ethiopia (Massowah, Meiso, Dire Daoua) (all BM), 2 ♂ 1 ♀ Sudan (Port Sudan; Kordofan: Jebel Angageh, Angageh Wells) (BM, MW).

Distribution. — The range of the species south of Jidda and Port Sudan: W., SW. and S. Arabia, Sudan, Ethiopia, Somaliland.

Subspecific characters. — A rather constant form. On the upperside well-marked, but all markings reduced as compared with ssp. *amenophis*, except the discal spots on the upperside of the hind wing. The discal spots in spaces 4 and 5 on the fore wing upperside minute or absent. Submarginal spots may be faint. Ground colour of hind wing underside dark greyish olivaceous, somewhat like ssp. *amenophis*, but sometimes more yellowish. ♂ (9—)10—11.6 mm.

Note. — Evidently overlooking the description by Walker, Butler (1884) described the same form under the name *Pyrgus evanidus* var. *adenensis* from Aden (holotype in the BM examined).

**Spialia doris evanida** (Butler)


Type-locality: Hub River (S. Baluchistan).

Material examined. — 17 ♂ 5 ♀: 1♂ 1 ♀ S. Iran (Ahwaz, Kerman) (BM), 13 ♂ 3 ♀ Sind (Hub River, type; Karachi, Hidrabad) (BM, MW, ML), 1♂ Cutch, 2 ♂ Punjab (Campbellpore), 1 ♀ Rajputana (Deesa) (all BM).

Distribution. — The eastern part of the range of the species, from S. Iran eastward.

Subspecific characters. — Above like ssp. *doris*, below like ssp. *doris* but ground colour paler, particularly in the hind wing which is pale yellowish. There exists, however, some individual variation, while some specimens are as dark as ssp. *doris*. Smaller than the latter, ♂ 8.6—10.2 mm.

Note. — Of the four subspecies recognized here, *doris* and *evanida* are most alike. Evans (1949) even considered the difference between them too small for subspecific recognition. However, the populations of ssp. *doris* and ssp. *evanida* appear to be entirely isolated geographically and I consider the subspecific distinction of *evanida* justified.

4. The *sertorius* species group

In the Palaearctic region the *sertorius* species group is represented by seven allopatric forms, externally clearly distinguishable, but the differences in the genitalia are almost
imperceptible or absent. These forms are: sertorius, ali, therapne, orbifer, hilaris, lugens and carnea. Whether one considers these forms subspecies or separate species (perhaps united into a superspecies) seems to be only a matter of taste, apart from the following considerations.

(1) therapne is the forma of Corsica and Sardinia. Kauffmann (1955) recorded the capture of sertorius at Evisa (Corsica). According to Bretherton (1966) sertorius was recently found in two places in Corsica, and Higgins & Riley (1970) state that specimens taken at Corte and Evisa have been described as intermediates of therapne and sertorius.

(2) The second generation of the North African ali looks very much like therapne, the difference being mainly the shape of the central spot and the colour on the underside of the hind wing.

(3) In sertorius, ali and therapne the shape of the central spot of the hind wing underside is angular; in orbifer, hilaris, lugens and carnea this spot is rounded.

(4) In Central and Eastern Europe the forms sertorius and orbifer must approach each other very closely and possibly overlap to a small extent. In Poland only sertorius is known (Bleszynski e.a., 1965; Krzywicki, 1970). The only orbifer specimens examined from Czechoslovakia originate from Jung-Bunzlau (Bohemia), farther I saw only sertorius from Czechoslovakia. According to Moucha & Novak (1960) only two reliable records of orbifer are known from Slovakia (Stúrovo, Kovačov), both near Hungary, while all other specimens collected in Slovakia belong to sertorius (see also Reiprich, 1960). The easternmost locality from where I have seen sertorius is Szobráncz, near the Czechoslovakian-Russian frontier.

Alberti (1965) said to have seen specimens with transitional characters from Northern Hungary in the Hungarian Natural History Museum, but the specimens of both sertorius and orbifer from the collections of this museum examined by me did not allow for such a conclusion. The boundary between sertorius and orbifer in Hungary appears to be the river Raba: all specimens collected west of it are sertorius (like all Austrian specimens), while east of the river only orbifer is known to occur.

In Northern Yugoslavia sertorius is widely, but locally distributed. I have seen specimens from the Sneznik (30 km north of Rijeka) and from Fuzine (15 km east of Rijeka). Prof. Lorković kindly informed me that sertorius has been captured at some more localities in northern Yugoslavia, viz. Zagreb and surroundings (Podsused, Samobor, Japetić), Klek near Ogulin, Hrvatsko (see also Lorković & Mladinov, 1971), Slunj, Ljeskovac (Plitvice lakes), Velika near Pozega, and Banja Luka. In the coastal region sertorius and orbifer appear to approach each other very closely. At Trieste only sertorius has been captured. Verity (1940) stated that orbifer occurs in Istria, but he did not give exact localities and the reliability of this record is doubtful. The northernmost locality in the coastal region from where I have seen orbifer is Senj (= Zengg). Koca (1901) recorded the same form from the nearby Krizpolje. Lorković (in litt.) found orbifer at Plitvice. Further south only orbifer has been collected (see also Lorković, 1973).

Rebel (1895) recorded specimens of the spring brood at Plitvice, with the spots on the underside of the hind wing of the sertorius type, but with the ground colour olive brown. It is not clear whether Rebel thought these specimens to belong to sertorius or to orbifer. Very probably they do not indicate a hybrid population. Lorković (in litt.) found several orbifer specimens at Plitvice and only one sertorius specimen, apparently without intermediate characters.
Thus, in spite of the close geographic vicinity of *sertorius* and *orbifer* the occurrence of intermediate populations has not yet been proved. According to the material available at present a possible hybridization is a rare event. This idea is supported by the discovery of differences between *sertorius* and *orbifer* in the larval and pupal stages in N. Yugoslavia (Lorković, 1973).

Exact localities in the border region of *sertorius* and *orbifer* from where I have seen specimens or reliable records have been represented in Map 5.

(5). Throughout Peninsular Italy only *sertorius* is found, but in Sicily it is replaced by an *orbifer* population with some *sertorius* features in the female (see under *Spialia orbifer*).

(6). The forms *hilaris* and *orbifer* and the forms *lugens* and *carnea* are connected by intermediates in SE. Turkey and the Samarkand region, respectively.

Of course, these arguments are not conclusive, but from the distribution and differentiation of *sertorius, ali* and *therapne* on one side and of *orbifer, hilaris, lugens* and *carnea* on the other, one may conclude that these forms fall taxonomically and geographically into two groups, viz. a western *sertorius* group and an eastern *orbifer* group.

![Female genitalia of *Spialia sertorius sertorius* (Chiciana, S. Spain). 21, ventral side; 22, left side; 23 right papilla analis](image-url)
For practical reasons I treat the two groups as species and I am uniting them into the superspecies *sertorius*. However, I must stress the fact that one could equally well consider *sertorius* and *orbifer* subspecies groups of one species. For the evolutionary and geographic history of superspecies *sertorius*, that shows the arrangement adopted to reflect the phylogenetic relationships, see Chapter 5.

In the Palaearctic no other representatives of the *sertorius* group exist. It is, however, surprising that there are two species outside that region which are apparently closely related to *sertorius* and *orbifer* and which show magnificently how the present type of valva of *sertorius* and *orbifer* has developed. One of these species viz. *mafa*, is African, and extends from South Africa to Abyssinia (Evans, 1937), SW. Arabia (Gabriel, 1954) and the vicinity of Mecca (material examined). The other species, *galba*, occurs throughout India, Ceylon and a part of Burma, and is also known from Hainan (Evans, 1949, 1956). Their valvae and gnathos are shown in Fig. 32—35. For the phylogenetic relations between *galba, mafa* and superspecies *sertorius*, see Chapter 5. From a broad point of view one could consider this species group a superspecies as the composing species are allopatric. However, by accepting a superspecies *sertorius* with the species *sertorius* and *orbifer*, it is impractical and obscuring history, to unite these species with *mafa* and *galba* into a single superspecies.

**Superspecies SPIALIA SERTORIUS** (Hoffmansegge)

**Taxonomy.**

It is not difficult to distinguish the species *sertorius* and *orbifer* with external characters. In *sertorius* the ground colour of the underside of the hind wing is red in various shades, from ochreous to a very vivid red, and the spots on the underside of the hind wing, particularly the central spot and the costal spot (in spaces 7—8) are more or less angular. In *orbifer* the ground colour of the underside of the hind wing is greenish or yellowish olive-grey, the spots are rounded and the costal spot is particularly distinct. Only in the subspecies *carnea*, *orbifer* can have a reddish underside of the hind wing, but as this subspecies is Asiatic it cannot be confused with *sertorius*.

In the male genital armature the difference between *sertorius* and *orbifer* is much less distinct. Moreover, the differential characters are subject to variation and not entirely reliable. The differences were discovered by Warren (1926), who emphasized their inconstancy. Kauffmann (1955) considered them too unreliable to be of any use, but this is slightly exaggerated.

The differences can be found in:

(a). Gnathos (Fig. 25, 27, 29, 31). The ventral spined part is narrowly pointed in *sertorius ali*, less narrowly pointed in *orbifer*, bluntly rounded in *sertorius therapne* and rounded in *sertorius sertorius*. Especially in *s. sertorius* the variation is considerable and specimens with a *therapne* or *orbifer*-like gnathos are not extremely rare. Further, the left and right parts of the gnathos may differ in form. Moreover, the angle from which the structure is observed, is important, an oblique position of the gnathos causing a more pointed appearance.

(b). Hairy fold at the inside of the valve. (Fig. 24, 26, 28, 30). In *orbifer* the ventral, horizontal part is usually best developed, in *sertorius* the horizontal and vertical parts are about equally well developed or the vertical part is best developed (*sertorius*...
Fig. 24—29. Inside of right valva and outside of left part of gnathos of Spialia. 24—25, *S. sertorius sertorius* (Hannover); 26—27, *S. sertorius ali* (Algeria); 28—29, *S. sertorius therapne* (Corsica)

ali). The variation in this character does not depend on the angle from which the fold is observed.

In the female genitalia of *sertorius* and *orbifer* (Fig. 21—23) I could not find clear differences.

From these facts it is obvious, that a possible hybrid between *sertorius* and *orbifer* cannot be detected by the genital characters, and only by the external ones.
Fig. 30—35. Inside of right valva and outside of left part of gnathos of *Spialia*. 30—31, *S. orbifer orbifer* (Turkey); 32—33, *S. mafa* (S. Africa); 34—35, *S. galba* (Ceylon)

*Spialia sertorius* (Hoffmansegg)

Nomenclature. — Apart from *sertorius*, two names have been used for this species, viz. *sao* Hübner and *hibiscae* Hübner. Warren (1926) pointed out that *Papilio sao* Hübner, 1800—1803, is a junior homonym of *Papilio sao* Bergstrasser, 1779, and that *sertorius* Hoffmansegg, 1804, is the correct name. However, Hemming (1936) recorded the name *hibiscae*, attributed by him to Hübner (1790—93). This name has been used in important publications, such as Verity (1940, 1947) and Kauffmann (1951). Evans
(1947) indicated that there is no evidence that the paper "Lepidoptera Linnei" where Hemming found the name *bibuscae*, had ever been published, so that the name *bibuscae* Hemming, 1936, should be placed as a synonym of *sertorius* Hoffmansegg, 1804.

Some authors (e.g. Lempke, 1953) have made an effort to alter the gender of the name *sertorius* in accordance with that of *Spialia*, resulting in the combination *Spialia sertoria*. This is incorrect, *sertorius* not being an adjective but a proper name.

Distribution (Map 6). — NW. Africa; from S. Europe northward to southern Bretagne (Picard, 1950), southern Netherlands, Osnabrück, Hannover and Harz Mountains, east to southern Poland (Krzywicki, 1970), the Czechoslovakian—Russian frontier, the river Raba in Hungary and Slavonia and Croatia in N. Yugoslavia. For details of the eastern distributional limits, see above and Map 5. *Spialia sertorius* occurs throughout Italy, Corsica and Sardinia, but in Sicily it is replaced by *orbifer*.

Habitat. — Flowery slopes, dry meadows from the lowlands up to 2200 m in the French Pyrenees Rouond (1932), to 2400 m in Spanish mountains (Manley & Allcard, 1970) and to 2300 m in Switzerland (Schmidlin, 1949). Mainly in xerotherm limestone environments, undoubtedly in relation with the requirements of the food plants.

Biolog. — Everywhere two generations a year, flying from April to June and from July to September, but in mountainous districts often monovoltine. The larva hibernates (Forster & Wohlfahrt, 1955).

Food plants: *Sanguisorba minor, Potentilla verna, Rubus idaeus* (Rosaceae) (Verity, 1940; Forster & Wohlfahrt, 1955). The food plants of the subspecies *ali* and *therapne* are unknown.

Geographic variation. — Three subspecies are recognized here.

**Spialia sertorius ali** (Oberthür)

Oberthür, 1881. — Etude d'Ent. 1 : 61, pl. 2 fig. 3.

Type-locality: Lambèse (Algeria).


Distribution. — Confined to NW. Africa.

Subspecific characters. — Male genitalia: gnathos ventrally narrowly pointed. External characters: first brood, ♂ 8.4—11.6 mm, underside of the hind wing red or pale brown with dark striae, at the termen alternating white and red or brown streaks, because the submarginal spots are modified, central spot with long projections towards base and termen; second brood: ♂ 8.3—10.3 mm, underside of the hind wing mostly yellowish red with less pronounced white markings, on the upperside of both wings the wite markings with a yellow shade.

Note. — The second brood is very similar to subspecies *therapne* and for this reason Oberthür (1910) gave it the name *therapnoïdes*. It can, however, easily be separated by the less warm ochreous red underside and by the central spot of the underside of the
hind wing, that in *therapnoides* has long projections towards base and termen (as in the first brood), while in *therapne* it only has a projection towards the termen.

**Spialia sertorius therapne** (Rambur)

Rambur, 1832. — Ann. Soc. Ent. France 1832 : pl. 7 fig. 4.
Type-locality: Corsica.

Material examined. — 54♂ 21♀ : 52♂ 20♀ Corsica (BM, ML, HO, HC), 2♂ 1♀ Sardinia (BM, ML).

Distribution. — Confined to Corsica and Sardinia.

Subspecific characters. — Male genitalia: ventral, spined part of gnathos not as narrow as in ssp. *ali*, blunt but not rounded as in *sertorius*. External characters: very small, ♂ 7.8—9.9 mm; on the underside shaded yellow, spots yellowish, submarginal spots very faint or absent. On the underside warm ochreous red, spots arranged as in ssp. *sertorius*; see also ssp. *ali*.

Note. — According to Higgins & Riley (1970) *therapne* is bivoltine, flying in April and September. However, I have only seen specimens dated from June to September.

**Spialia sertorius sertorius** (Hoffmansegg)

Type-locality: Germany.

Material examined. — 779♂ 420♀ : 36♂ 13♀ Portugal (BM, ML), 49♂ 14♀ S. Spain (BM, ML, ITZ), 101♂ 33♀ C. and N. Spain (BM, ML), 10♂ 3♀ Spanish Pyrenees (BM, ML), 92♂ 45♀ French Pyrenees (Hautes Pyr., Pyr. Or.) (BM, ML, ITZ), 231♂ 148♀ France (BM, ML, ITZ), 13♂ 8♀ Belgium (BM, ML), 12♂ 10♀ Netherlands (ML, ITZ), 44♂ 16♀ Switzerland (BM, ML, ITZ), 34♂ 14♀ Germany (Bayern to Hannover and Leipzig) (BM, MB, ML, ITZ), 39♂ 35♀ Austria (BM, ML, MB), 7♂ 8♀ Czechoslovakia (Praha, Slany, Hlubočep, Trencsén, Eperjes, Szobráncz) (MB, ML, BM), 1♂ 1♀ Hungary (Sopron, Magyarovár) (MB), 12♂ 4♀ N. Italy (BM, ML, ITZ), 84♂ 63♀ C. Italy (BM, ML), 1♀ Elba (ML), 2♂ 1♀ Calabria (BM), 10♂ 2♀ Trieste and Istria (BM, ML, MB), 1♀ Slovenia (Sneznik) (ML), 1♂ 1♀ Croatia (Fuzine) (ML).

Distribution. — The whole distribution area of the species, except NW. Africa and Corsica-Sardinia, i.e. West, Central and South Europe, east to Slavonia and E. Czechoslovakia; for details, see above and Map 5.

Subspecific characters. — Male genitalia: ventral, spined end of gnathos broad and rounded. There is some variation in the direction of ssp. *ali* and ssp. *therapne*, but these forms are rarely equalled. External characters: on the underside of the hind wing the submarginal spots not modified as in ssp. *ali*, ground colour red in various shades to ochreous red or, less commonly, yellowish, particularly in the second brood in S. Europe. The two broods differ in size: first brood♂ 10—12 mm, second brood♂ 9—11 mm, but there is much variation and a general rule cannot be given.

Variation. — This subspecies is rather variable, especially in Spain. Some authors, e.g. Verity (1940), have recognized several subspecies or "races". At least partly, this
Map 5. Distribution of *Spialia sertorius* and *orbifer* in Central and Southeastern Europe. ● = *sertorius*, material examined; O = *sertorius*, literature records; ▲ = *orbifer*, material examined; △ = *orbifer*, literature records.
variation does not seem to be geographic, but it is possible that some geographic variation exists. The following variation is known:

(1). The spots on the upperside may be all present and well-marked or may be reduced. Particularly the submarginal spots can be totally absent. Based on this variation Verity (1940, 1947) and Kauffmann (1951) recognized the subspecies *hibiscae* (by Verity attributed to Hübner, by Kauffmann to Hemming; see also above, under Nomenclature) (well-marked) and *sertorius* (markings reduced). The second brood of both forms is somewhat smaller than the first brood and has been named *parvula* Verity (for *sertorius*) and minor Rebel (for *hibiscae*).

Both Verity and Kauffmann state that the dark form (*sertorius*) is confined to humid places; therefore, it can hardly be assigned subspecific state. There are still more reasons to mistrust the correctness of the subspecific separation. In most places both forms occur together, connected by many transitions. I have seen both forms from Lisbon, the Pyrenees, the Basses Alpes, Belgium, the Netherlands, Germany and Lower Austria. Mostly *hibiscae* is the dominant form, but *sertorius* can dominate in some localities (and perhaps only in some years). Bergmann (1952) found proportionally more *hibiscae* when the years were drier.

Lempke (1953) is correct in stating that in the Netherlands the dark form dominates, but he also mentions better marked specimens and says (p. 244): “Such specimens agree totally with subsp. *hibiscae* Hemming (…). It is difficult to name such specimens as, with us, they belong to the infrasubspecific category, while the name was given to a group of higher rank. Nomenclaturally these limits are, of course, splendid, but in practice all limits disappear.” However, in this case as well as in many others the difficulties arise from a wrong interpretation of the facts and a wrong concept of superspecies. In the present case, *sertorius and* *hibiscae* are not separate subspecies, but climatic forms. Consequently, I do not recognize *hibiscae* as a separate subspecies.

(2). Mostly, the ground colour on the underside of the hind wing is red or reddish, but in southern populations the colour may be ochreous yellow or even pale yellow. A yellow colour can also occur in the second brood in northern populations. The cause of this variation is unknown. As the yellow colour is not confined to any particular region, it cannot be used as a subspecific character.

(3). Particularly in southern regions there is a great variation in size, which is partly individual, partly geographic. In Spain larger and smaller specimens fly together (Warren, 1926). According to Zerny (1927), three size categories can be distinguished in the vicinity of Albarracín. This suggests that no transitional specimens occur, but that is not true. The difference can be very large: four males from San Ildefonso (Segovia, June to August) measured 9.8, 10.1, 12.2 and 13.1 mm, four females from the same locality 10.2, 13.1, 13.4 and 14.2 mm (BM).

In Peninsular Italy, except S. Calabria, all specimens are small, first brood ♀ 9.7—11 mm, second brood ♀ 8.4—10.1 mm. In N. Italy and S. Calabria the specimens measure as much as 12—13 mm.

(4). Some minor variation exists as mentioned below. Apart from *sertorius* and *hibiscae* the following forms have been described as “races”:

(a). *gracilis* Verity, 1921 (type-locality: Florence). The small form of Peninsular Italy; on the upperside spots small but all present; underside of the hind wing red or pale yellow, with relatively few transitional specimens. The first generation (for measurements see above, under (3)) was named *subgracilis* by Verity (1921). This form is rather
constant in Italy, although the larger specimens of the first brood cannot be distinguished from *bibiscae*. In Spain *gracilis* occurs together with larger specimens, in France it occurs only in dry places in the south. Small specimens with pale underside of the hind wing were already known under the name *eucrata* Ochsenheimer, 1805. Such specimens can also be found in the second brood in northern populations.

At the moment I do not know how to place the form *gracilis*. As it does not seem to have a distributional area of its own, it appears inappropriate to give it subspecific rank. Nevertheless, it is not impossible that *gracilis* originated by geographic isolation (see also Chapter 5).

Note. — Verity described *gracilis* already in 1919 as the second generation near Florence. According to the International Code of Zoological Nomenclature, Article 45d, the original status of *gracilis* is determined as infra-specific. However, in 1921 Verity clearly applied the name to a particular geographic area and he called *gracilis* a “race”. Therefore, the subspecific status of the name dates from 1921.

(b). *guadarramensis* Warren, 1925 (type-locality: La Granja, Sierra de Guadarrama). The largest form known, according to Warren (1925) 30—31 mm (centre of the thorax to tip of the fore wing x2). I saw only one female from the type-locality, that measured 14.2 mm. Furthermore, the form is characterized by the ground colour of the underside of the hind wing, which is vivid red, much deeper in shade and more brilliant than in Central European specimens. This, too, is the case in the single female seen from La Granja. However, as stated by Warren, *guadarramensis* occurs together with normal-sized and small specimens. I saw two males from Sierra de Guadarrama that were almost of the size of *gracilis*. Moreover, not all large specimens from Central Spain are richly coloured, e.g. the large male and female from San Ildefonso mentioned above (under (3)) have the ground colour of the hind wing underside dark yellow and brick red, respectively.

Like *gracilis*, this variety cannot be defined as a subspecies.

(c). *gavarniensis* Warren, 1926 (type-locality: Gavarnie). According to Warren, almost all specimens in the vicinity of Gavarnie (Hautes Pyrénées) differ from ssp. *sertorius* in the warm yellow-brown, almost orange colour of all parts of the underside, which are white in ssp. *sertorius* with the exception of the white spots. The ground colour of the underside of the hind wing of *gavarniensis* is brighter red than of *sertorius*.

Indeed, most specimens from Hautes Pyrénées show this type of variation, but rarely in an extreme form and many specimens are practically indistinguishable from Central European *sertorius*.

I have seen a female from Ordesa, at the Spanish side of Cirque de Gavarnie, that looked like *gavarniensis*, but another female and two males from the same locality did not show the colour that is typical for *gavarniensis*.

The cause of this variation which is confined to the Central Pyrenees, is unknown. It is not very likely that it originated during geographic isolation, as at least at present *sertorius* is wide-spread in the Central Pyrenees, flying from the lowlands up to 2200 m. At any rate it originated postglacially, as the Pyrenees were uninhabitable for *sertorius* during glacial periods. For this reason and for the fact that in the context of the total variation of the species *gavarniensis* is only an unimportant minor variety, it is undesirable to give it the same rank as the forms *ali* and *therapne*. I am placing it here as a local form.

(d). *dioides* Verity, 1926 (type-locality: Oulx, Cottian Alps). Central spot on the underside of the hind wing large with projections towards base and termen. Ground
colour of the underside of the hind wing ochreous or yellowish, whitish along termen, veins outlined in a paler shade. Upperside as ssp. *sertorius*, but the specimens are larger, up to 13 mm. Such specimens occur in the western Alps, but mostly the colour of the underside of the hind wing is red or ochreous red and all transitions to *sertorius* occur. This form seems to be still less sharply defined than *gavarniensis* and I regard it also a local form.

According to Verity (1940) the same form occurs in S. Calabria. I have seen only 2 ♂ and 1 ♀ from S. Calabria and these specimens looked like *sertorius* with some variation towards the Sicilian *orbifer*.

**Spialia orbifer** (Hübner)

Distribution (Map 6). — Sicily; from N. Yugoslavia, Hungary and Czechoslovakia eastward through S. Russia and S. Siberia to the Amur region and N. Thibet (Sining) and through the Balkans and Turkey to Baluchistan and Afghanistan from where it goes north through Turkestan to S. Siberia.

The distribution limits are badly known. For the distribution in E. Europe, see above and Map 5. Although it is very probable that this distribution is continuous, there are no records from large intervening areas in Russia and Siberia. From Russia we have the observation of Caradja (1895), that *orbifer* is widely distributed in SW. Russia and the Volga region, further the record of Eversmann (1844), who mentioned it from Saratov on the Volga. Krulikowsky (1908) recorded *orbifer* from Kasan and Spassk, but he only relied on some literature records. The species is known from the Crimea (Melioransky, 1897; Korshunov, 1964; material examined), the Caucasus and Transcaucasia (Romanoff, 1884; Alberti, 1969), but in the S. and SE. Russian steppe region it is apparently rare, as it is not mentioned, e.g., by Obraztsov (1936) from the Transdnjepr region, neither by Alberti & Soffner (1962) from S. Russia, nor by Gross (1925) from Chwalynsk on the Volga.

From the W. Siberian lowlands it is only recorded by Sjtsjuko (1916) from Tjumen.
Further east it is known from the upper Irtysh (Lederer, 1853), Altai and Kentsi (Elwes, 1899; material examined) and it is widely distributed though uncommon in the Amur region and the Maritime Province (Staudinger, 1892; Kurentzov, 1949, 1970). Matsumura (1927) and Bryk (1946) did not record orbifer from Korea, but Sugitani (1936, see Evans, 1949) described the form munasuki from that country. In China it is undoubtedly much more widely distributed than is suggested by the few localities known (Shansi, S. Shensi, Sining; see material examined).

In the southern Palearctic orbifer is widely distributed. The southernmost localities are: vicinity of Jerusalem (Graves, 1925; material examined), Bished (Iran) (Forster, 1939) and Ziarat (W. Pakistan) (material examined). Through Afghanistan, Transcaspia and Turkestan to the Ilī region (Alphéraky, 1881; Wagner, 1913) and possibly continuously to the Altai. For details, see below.

Habitat. — Like the habitat of Spialia sertorius. In Macedonia I found orbifer up to 2000 m, in C. Anatolia it flies up to 1400 m (Pfeiffer, 1927), in Chitral it is not rare at 4000 m (Evans, 1927).

Biology. — Bivoltine in the western part of the area, west of Iran. According to Pfeiffer (1932) a third brood occurs near Marash (E. Turkey), but Graves (1925) is of the opinion that late specimens may rather be of the second brood, but delayed by the summer pause. Evans (1949) assumed that the Asiatic populations (from Transcaspia eastward) are single-brooded.

The larval stages remained unknown till, very recently, Lorković (1973) succeeded in rearing this species on Sanguisorba minor (Rosaceae).

Geographic variation. — Apart from the variation in number of broods per year, the species varies in size, colour and markings. The variation in C. and E. Asia is still badly known and with more material available subspecies lugens may prove to be heterogeneous.

**Spialia orbifer orbifer** (Hübner)


Type-locality (designated here) : Hungary.

Material examined. — 424 ♂ 187 ♀ : 10 ♂ 6 ♀ Sicily (Messina, Castelbuono in Madonie, Palermo, Etna-Randazzo) (BM), 1 ♂ "Istria" (ML), 55 ♂ 27 ♀ Hungary (Öskü, Fenyőfő, Gyenesdiás, Szár, Ugod, Pilisvörösvár, Sümeg, Akali, Budapest) (MB, ML, BM), 1 ♀ 1 ♀ Bohemia (Jung Bunzlau) (BM), 7 ♂ 1 ♀ Croatia (Zengg=Senj) (BM), 10 ♂ 7 ♀ Bosnia (BM, ML, ITZ), 1 ♂ Hercegovina (ML), 9 ♂ 7 ♀ Dalmatia (BM, ML, ITZ), 81 ♂ 26 ♀ Yugoslavian Macedonia (ML, HC, ITZ), 102 ♂ 60 ♀ Greece (BM, ML, ITZ), 1 ♂ Crimea (BM), 143 ♂ 48 ♀ Turkey (European and Asiatic) (BM, ML), 3 ♀ Russian Armenia (Vartian), 3 ♂ 1 ♀ N. Iran (N. of Teheran) (BM, Vartian).

Distribution. — The western part of the range, eastward to W. Siberia, south-eastward to N. Iran (north of Teheran). Also in Sicily.

Subspecific characters. — Bivoltine. First brood, ♂ 11—12.6 mm, second brood, ♂ 8.4—11 mm. Markings on the upperside variable, sometimes all spots present, sometimes they are very reduced, particularly the submarginal spots. Ground colour on the underside of the hind wing greenish to ochreous olivaceous.

Variation. — The name minor Rebel, 1909, for the second brood of Spialia sertorius,
is also suitable for the small brood of orbifer. In a series of about 50 specimens collected in Mavrovo (Yugoslavian Macedonia) in the first half of July, the males measure 10.5—12.2 mm. As the specimens were collected between 1000 and 2000 m, it seems possible that a single brood exists there (and perhaps in other mountain regions).

A dark, less marked form was described as tesselloides by Herrich-Schäffer (1845) from Sicily. Verity (1940) gave some confusing remarks about the type-locality. Evidently, he did not examine the original description by Herrich-Schäffer and relied entirely on Keferstein (1851: 326). The latter only mentioned that tesselloides occurs in "Türkei", without stating that it does not occur elsewhere. Herrich-Schäffer received the type specimens from Keferstein and he clearly stated that they originated from Sicily. Verity supposed that Herrich-Schäffer gave "S. Europe" as type-locality and that this was corrected by Keferstein in "Turkey". As this form occurs in Turkey, Saloniki, the Olympus and Sicily (according to Verity), the problem is not very important.

The smaller second brood of tesselloides was named posttesselloides by Verity (1938) after specimens from the Olympus. Evans (1949) correctly placed tesselloides as a name relating to orbifer, but his opinion that posttesselloides is a synonym of sertorius is an apparent mistake.

This dark form bears the same relation to the better marked nominate form, as the form sertorius does to the well-marked form bibisc ae. Also its valuation must be the same, as both forms occur together on the main part of the distribution area, tesselloides perhaps dominating in some districts, but without a distribution of its own and connected with better marked specimens by innumerable transitions.

From the point of view of geographic history the occurrence of orbifer in Sicily is highly interesting. The species seems to be scarce there. Verity (1940) saw only two Sicilian specimens which he attributed to the form tesselloides. Indeed, all Sicilian males in the BM are dark on the upperside, but the females are somewhat more distinctly marked (this is a normal feature in orbifer). The hind wing underside of the males is of the colour and markings of orbifer, but the central spot is rather angular. The females, however, vary from ochreous to red and the central spot is very suggestive of sertorius. The measurements are: ♂ 10.5—12.7 mm, ♀ 12.2—15.8 mm. In all, it seems advisable to refer the specimens to orbifer, but they suggest a hybrid population rather than pure orbifer.

**Spialia orbifer hilaris** (Staudinger)


Type-locality: Mardin (SE Turkey).


Distribution. — From SE. Turkey southward, to Matta (15 km SW. of Jerusalem; material examined) and Amman (Jordan; Hemming, 1932b) and eastward to Kerman- shah (W. Iran; material examined).

Subspecific characters. — Bivoltine. First brood ♂ 10.8—13.8 mm, second brood
♂ 9—11.3 mm. On the upperside, the markings are more conspicuous than in ssp. orbifer, particularly the submarginal spots.

Variation. — The small second brood was named secunda by Graves (1925). In NW. Syria (Akbès) also less conspicuously spotted specimens occur which form a transition to ssp. orbifer.

Note. — If compared in series ssp. hilaris is quite distinct from ssp. orbifer. Its distribution, however, suggests, that it is a climatic form, adapted to hot and dry conditions, rather than a subspecies (though climatic forms and subspecies are, of course, not mutually exclusive). Provisionally I follow common use by considering hilaris a subspecies. It would be interesting to have more material from the contact zone between the subspecies orbifer and hilaris in order to study a possible clinal variation along a temperature and/or drought gradient.

Spialia orbifer lugens (Staudinger)

Type-locality: Ferghana.

Material examined. — 71 ♂ 19 ♀ : 3 ♂ NE. Iran (Khush Yailaq) (WLB), 2 ♂ 1 ♀ Transcaspia (Merv, Achal-Tekke) (BM), 1 ♂ Bokhara (BM), 8 ♂ 5 ♀ Samarkand (BM, ML), 1 ♂ Hissar Mts. (ML), 5 ♂ 2 ♀ Ferghana (Namangan, Margelan, Gultscha) (BM), 24 ♂ 4 ♀ Naryn (BM, ML), 9 ♂ 1 ♀ Talass Ala-Tau (ML), 1 ♂ Tashkent (ML), 1 ♂ Alexander Mts., 1 ♂ 1 ♀ Issyk-kul, 2 ♂ Tianshan, 3 ♂ Altai (Ongodai), 1 ♂ Amur region (Tjutju-ho), 5 ♂ 4 ♀ Shansi, 3 ♂ S. Shensi, 1 ♂ 1 ♀ Sining (all BM).

Distribution. — The whole Asiatic range of the species east of the Caspian Sea, except Afghanistan and from Baluchistan to Chitral.

Subspecific characters. — Monovoltine. Large, ♂ and ♀ to 14.6 mm, and dark on the upperside, submarginal spots mostly faint, may be absent, but sometimes (mainly in females) well-developed. On the underside of the hind wing indistinguishable from ssp. orbifer.

Variation. — Size is variable, large specimens are found in China, ♂ 12.6—14.6 mm, and in the Talass Ala-Tau, ♂ 13.3—14.1 mm, specimens from Naryn are somewhat smaller, ♂ 11—13.7 mm, the few males from the Altai measure only 11.9—12.6 mm. Therefore, one can also refer the Altai specimens to ssp. orbifer, at least with regard to their size.

Wagner (1913) remarked that orbifer occurred in the Ili region “sowohl in typischen Stücken, als auch in der grösseren und dunkleren var. Lugens Stgr.” He also mentioned specimens with large spots which he called “var. Hilaris Stgr.”. From these facts it seems possible that the subspecies orbifer and lugens meet in N. Turkestan and the Altai.

In some females from the province of Samarkand, the ground colour of the underside of the hind wing is reddish brown instead of greenish. Although such specimens have the submarginal spot in spaces 4 and 5 at the underside of the hind wing well-developed (unlike the usually less conspicuous spot in ssp. carnea), they are suggestive of ssp. carnea. Possibly there is a large transitional zone between the subspecies lugens and carnea. However, while I have seen ssp. lugens from Merv and the Achal-Tekke region, ssp. carnea is recorded from the vicinity of Herat in W. Afghanistan (Clench &
Shoumatoff, 1956).

Unfortunately, the material from N. Iran is too scarce to allow for a statement about the contact zone between the subspecies orbifer and lugens. Three males from the mountain Khush Yailaq in the eastern part of the Elburz Mountains are indistinguishable from lugens specimens from Turkestan. Two males and one female from Derbend and Vanak (N. of Teheran), about 400 km west of Khush Yailaq, look like orbifer specimens from more western localities, without any trace of the influence of ssp. lugens.

Spialia orbifer carnea (Reverdin)

Reverdin, 1927. — in Bang-Haas · Horae Macrolep. 1 : 52, pl. 7 fig. 28.  
Type-locality: Paghman Mountains (Afghanistan).

Material examined. — 36 ♂ 14 ♀ : 15 ♂ 5 ♀ Baluchistan (Ziarat, Urak, Old Urak) (BM), 4 ♂ 3 ♀ Afghanistan (Paghman Mts., Ararp, both W. of Kabul; Panjshir Valley, N. of Kabul) (BM, ML), 14 ♂ 5 ♀ Chitral (Chitral, Shandur plateau) (BM, CW), 3 ♂ 1 ♀ Gilgit (Ghizar, Halttar, Gilgit) (BM).

Distribution. — Afghanistan and from Baluchistan (vicinity of Quetta) to Chitral.

Subspecific characters. — As ssp. lugens, but on the underside of the hind wing warm red to brown-yellow. ♂ 12.2—14.2 mm, ♀ 13.6—16.4 (!) mm. In most specimens the submarginal spot on the underside of the hind wing in spaces 4 and 5 is less conspicuous than in other subspecies.

Variation. — On the upperside, the spots are variable, the submarginal spots may be well-developed, but are sometimes totally absent (Chitral).

5. Evolutionary and Geographic History of the Genus Spialia in the Palaearctic Region

a. General

In this chapter we will attempt to trace the evolutionary history of Spialia in the Palaearctic by analyzing some characters as to their plesiomorphous (primitive) or apomorphous (derived) condition (Hennig, 1966). The conclusions arrived at may serve for the reconstruction of the geographic history. The reconstruction of the evolutionary and geographic history forms the theoretical basis for the arrangement of the species and subspecies adopted in the preceding chapters.

The phlomidis and sertorius groups will be dealt with separately. Their phylogenetic relationship cannot be treated without a revision of the whole genus.

b. The phlomidis group

1. Evolutionary history.

We will at first examine the characters that are peculiar of the phlomidis group in order to show that the arrangement adopted in this paper is phylogenetically correct. Thereafter, we will try to detect the evolution within the phlomidis group.

(1). Valva. In the phlomidis group the cucullus is strongly spined at its apex. In the rest of Spialia this character only occurs in spio, but less strongly developed. In the
other Spialia species the cucullus is quite different, more or less concave dorso-distally and often forms a flap so as to envelop partly the costal process; spines as in the phlomidis group are absent, but sometimes the rim of the flap or the extreme apex of the cucullus is slightly indented. If we assume that the cucullus originally was a plain structure, merely the ventral thickening of the valva, the phlomidis type with its bent and spined apex is an apomorphic stage of the original, simple cucullus, just as the type of cucullus with a flap is its apomorphic stage (but apparently developed at a later time; this however, falls outside the scope of this paper).

Unless we assume that this character arose independently in the species of the phlomidis group and in spio, the phlomidis group plus spio can be considered a monophyletic group, as the species share the same apomorphic condition of the cucullus and as they comprise all species with this condition.

(2). Aedeagus. Outside the phlomidis group a sclerotized excrescence of the aedeagus is rare in Spialia. This part occurs in e.g. nanus and abscendita as a short, spined ventral branch, quite different from the latero-ventral crest or branch (somewhat to the left), found in the phlomidis group. Moreover, in the phlomidis group the distal end of the aedeagus is bent downward to the left and strongly developed, a unique feature in Spialia. Undoubtedly, an excrescence points to an apomorphic condition with regard to the situation where this structure is absent. Evidently, it evolved in the phlomidis group and in nanus and its allies along different lines. Also the type of apex found in the phlomidis type of aedeagus must be the apomorphic condition and the simple, straight aedeagus the plesiomorphic one.

So again we can state that the phlomidis group is monophyletic, but now spio falls outside the group.

(3). Antevaginal structures. The large, wing-like structures of the phlomidis group are unique in Spialia, but in spio a less developed type is found. The presence of such specialized structures appears to be an apomorphic condition as compared with their absence (3a) and the strong development in the phlomidis group appears to be an apomorphic condition as compared with the weak development in spio (3b).

Again, we find that the phlomidis group is monophyletic and that spio must be included, if we draw the limits more broadly.

Summarizing, it appears justified to call the species of the phlomidis group monophyletic, originating from a common ancestor and comprising all progeny of that ancestor known. Spialia spio is phylogenetically related to the phlomidis group, but it does not share the apomorphic condition of some characters. For this reason and for its distribution (Ethiopian against the eremian regions of the Palaearctic for the phlomidis group) spio can better be left out of the phlomidis group.

Now, we will try to trace the evolution within the phlomidis group.

(4). Aedeagus. The excrescence of the aedeagus forms a crest in phlomidis, doris and osthelderi and a branch in geron. We may assume that an outgrowth evolves from small to large. Thus the situation in geron is the apomorphic condition and the crest, the plesiomorphic one.

(5). Cucullus. The apex of the cucullus is scarcely bent in phlomidis but strongly bent in the other species. Apparently, the larger the bend, the more advanced the evolution. Thus the strongly bent condition appears to be apomorphic.

(6). Costa of valva. The costa is dorsally more or less densely set with small spines in osthelderi, geron and doris, smooth in phlomidis. These spines are unique in Spialia.
They appear to represent the apomorphous condition with regard to the smooth dorsal surface of the costa.

(7). Costa of valva. In *doris* the distal end of the costa is concave. This appears to be a further differentiation of the costa that originally was only a thickening of the dorsal ridge of the valva. Consequently, the condition in *doris* is apomorphous.

(8). Markings on the underside of the hind wing. The direction of the central band on the underside of the hind wing is rather variable in *Spialia*, but usually the band is connected with or directed to the outer spot in space 7 or to a point between the outer and inner spots in space 7. In *spio*, *osthelderi*, *geron* and *doris* the central band is directed to the outer spot in space 7 or somewhat more to the base, in *phlomidis* it is connected with the inner spot in space 7. The lastnamed condition appears apomorphous, unless we assume that the other condition arose independently in several species.

(9). Ground colour of the underside of the hind wing. In *Spialia* this ground colour
is never white or whitish, except in osthelderi osthelderi. Evidently, the white colour is the apomorphous stage. As mentioned above (chapter 3) the same character occurs in the same region in some other Hesperiidae.

(10). Costa of the valva. In the phlomidis group the ventro-distal end of the costa bears strong spines, except in geron geron. Generally, the absence of spines on the valves in Spialia appears to be a less differentiated, plesiomorphous condition. In the case of g. geron, however, we must suppose that the spines have been lost, for the following reason. In Spialia usually the ventral or ventro-distal part of the costa is differentiated with spines or brushes. In phlomidis, doris, osthelderi and geron struwei the position and development of the spines is the same and in spio we find the same spines about the middle of the ventral side of the costa. The situation in spio appears to be less differentiated (in Fig. 36 indicated by 10a). It is most unlikely that only in geron geron the original unspined condition was maintained, as this would contradict other characters and the spined condition would have evolved independently in some or all other forms. So we may assume that the condition in geron geron is apomorphous as compared with the condition in the other species of the group (in Fig. 36 indicated by 10b).

In Fig. 36 the supposed evolution of the phlomidis group is summarized and the plesiomorphous and apomorphous conditions of the characters dealt with are represented symbolically.

The subspecific differentiation of phlomidis and doris does not need to be dealt with here; see chapter 3 and, for doris, see also below.

2. Geographic history.

The species of the phlomidis group have a peculiar distribution: they occur in the eremian parts of the Palaearctic. Although there exists some overlap, the phlomidis group forms geographically a link between the sertorius group and the African Spialia species. However, as will be shown below, the phylogenetic link between the sertorius group and its African congeners has nothing to do with the phlomidis group.

In the last paragraph spio was shown to be the probable phylogenetic connection between the phlomidis group and the African Spialia species. Moreover, spio appears to have retained more characters of the supposed common ancestors than the species of the phlomidis group. This does not necessarily mean that the phlomidis group has an Ethiopian origin, it only makes probable that the development within the group is of a rather recent time. From Fig. 36 it follows that the most recent development was the separation of doris, osthelderi and geron, the most eremian species. This makes it probable that the desiccation of the southern Palaearctic and the broadening of the eremian zone in this region have played a part in the evolution of the phlomidis group, as the common ancestor of doris, osthelderi and geron may have been forced to adaptations to a very dry environment. However, once eremian, this supposed species must have suffered more from wet than from dry periods. Thus, the Pleistocene Pluvial Periods (cf. Moreau, 1955) have undoubtedly been important for the evolution of the phlomidis group by causing geographic isolations. It is, however, impossible to date or to locate more or less exactly the isolations that necessarily have started the evolution of the phlomidis group. This is due to our very incomplete knowledge about both the phlomidis group and the history of the regions concerned. Undoubtedly, the Zagros Mountains, the Mesopotamian plains and the Nile Valley have at some time played a part in the
geographic history of the *pblomidis* group, but this part is not clearly discernible, at least at the specific level. The subspecific differentiation of *doris* and *osthelderi*, however, appears to be clearly influenced and probably caused by a Pluvial Period that moistened the Zagros Mountains and made it possible for forests to develop in the Mesopotamian plains. Also an inundation of the latter region by transgression of the sea may have had influence. Thus, we have a western and an eastern subspecies in *osthelderi* (ssp. *osthelderi* and ssp. *gecko*, respectively) and a western group of subspecies and an eastern subspecies in *doris* (ssp. *doris* + *amenophis* and ssp. *evanida*, respectively). It is confusing that *doris doris* and *doris evanida* are so much alike and *doris amenophis* so different, as one is easily inclined to suppose the closest relationship between forms that resemble each other most closely. However, the large spots of *doris amenophis* are undoubtedly apomorphous; thus the resemblance between *doris doris* and *doris evanida* is based on a plesiomorphic character. As clearly pointed out by Hennig (1966), correspondence in plesiomorphic characters is no measure for phylogenetic relationship.

The distribution of *doris amenophis* suggests that the Nile is, and probably has been in the past, a distributional barrier, as *doris amenophis* is not known from the area west of the Nile. The occurrence of an isolated population of *doris* far to the west, in Morocco (*doris daphne*) shows that *doris* once had a larger distribution in N. Africa. As it is unclear why a species adapted to desert environment would die out in the desert, the lack of specimens of *doris* from the region between Morocco and Egypt may be rather the result of poor exploration than of true absence.

1. Evolutionary history.

We will deal with the characters in the same way as in the foregoing paragraph.

(1). Valva: costal process. In *Spiidia* the costal process usually consists of a ventro-distal thickening of the costa, with hairs or spines. This structure may be very differentiated and is often roofed in by a fold from the dorso-distal part of the costa. The type found in *sertorius* and its allies, viz., an appendage of the ventro-distal part of the costa, set with spines that are upturned and directed to the dorso-distal part of the valva, is not found elsewhere. Such a differentiated structure seems to be apomorphous rather than plesiomorphous. The plesiomorphous stage of this character is difficult to indicate in the other *Spiidia* species, as most species appear to be rather differentiated. It is probable that the plesiomorphous stage of the *sertorius* type of costal process is no longer in existence. The most important statement, however, is that the resemblance between the species of the *sertorius* group in this case is based on an apomorphous character. An independent development of this character in various species in very unlikely.

(2). Valva. In the species of the *sertorius* group, and only in these species, the inside of the valve is provided with a conspicuous, hairy fold. This must be an apomorphous character as it is absent in all other *Spiidia* species, as well as in related genera.

(3). Female genitalia: 8th abdominal segment. In the *sertorius* group the ventral and dorsal sclerites of the 8th abdominal segment are fused together so that the sclerotization of the segment consists of two parts that dorsally are connected by a membrane and ventrally by a narrow sclerotized antevaginal band. In other *Spiidia* species the 8th abdominal segment bears four sclerites that are hardly or not fused together. The fusion of sclerites can be taken as an apomorphous character.
(4). Gnathos. All species of the sertorius group have a well-developed gnathos. In superspecies sertorius the strong differentiation into a stalk and a spined "head" appears to indicate an apomorphous stage as compared with the slighter differentiation in mafa and galba.

(5). Valva: costal process. If we imagine the evolution of the costa in Spialia from a plain structure towards a structure with highly differentiated appendages, there can be seen a gradual development of the costa in the sertorius group: from mafa through galba to sertorius and orbifer the costal process is shifted as it were towards the distal end of the costa and, eventually, replaces it. The difference between mafa and galba is slight as compared with the difference between galba and sertorius. So we can call the sertorius type the apomorphous stage and the mafa/galba type the plesiomorphous stage.

(6). Valva. The hairy fold at the inside of the valva shows different forms. There appears to be a gradual change from mafa through galba and sertorius to orbifer as the fold changes its position in that direction from horizontal-dorsal through vertical to horizontal-ventral. Possibly the development of the fold has run parallel to that of the costal process, but this cannot be more than an assumption as it is yet impossible to indicate the apomorphous and plesiomorphous stages of the position of the fold. Thus, we cannot use this character for the reconstruction of the evolution of the sertorius group.

(7). Tegumen and uncus. In mafa and galba there is an area between the uncus and the tegumen that is only weakly sclerotized, thus forming a more or less triangular "fenestra". In superspecies sertorius this "fenestra" is absent, though the connection between the uncus and the tegumen is clearly visible. The phylogenetic importance of this "fenestra" is still obscure. It may indicate that mafa and galba are closely related, as it is possible that the "fenestra" is an apomorphous character, but this statement is not very well founded at the moment. If also other characters are included, we may suppose that it is desirable to unite mafa and galba into a superspecies. This, however, falls outside the scope of this paper.

(8). Colour of the underside of the hind wing. In Spialia this underside shows various colours, mostly greenish or ochreous. In sertorius the colour is red or reddish ochreous, in orbifer it is greenish, but in orbifer carnea it is as red as in sertorius sertorius. The red and reddish ochreous tinges seem apomorphous if compared with the greenish colour. However, the red colour must have originated independently in sertorius and in orbifer carnea, as other characters (e.g. position of the hairy fold of the valva, measurements, spotting) show that orbifer carnea is an orbifer lugens with a red underside of the hind wing.

We can also suppose a parallel development of the red colour in the subspecies of sertorius, but this assumption is not supported by other characters (e.g. hairy fold, spotting). So we may assume that the red colour originated twice. In Fig. 37 this is indicated by the numbers 8a and 8b.

(9). Spotting on the underside of the hind wing. This is very variable in Spialia, some species having distinct spots, others straight or curved bands. If there is a distinct central band, this band is directed to or conjoined with the outer spot in space 7 or it is directed to a point between the inner and outer spots in space 7. It is, however, directed to or connected with the inner spot in space 7 in sertorius and orbifer and in phlomidis. As stated above, the situation in phlomidis can be considered apomorphous. Also the situation in superspecies sertorius can be called apomorphous. Apparently the resemblance
between *phlomidis* and superspecies *sertorius* in this respect is based on a parallel evolution. In Fig. 37 the character of the direction of the central band is indicated by the number 9a.

A main differentiating character between *sertorius* and *orbifer* is the shape of the central spot on the underside of the hind wing. This spot is angular in *sertorius* and rounded in *orbifer*. If a continuous central band is broken into spots by darkening of the veins one expects that the central spot is angular along veins 4 and 6, while these angles may become rounded off. This appears to have been the case in superspecies *sertorius*, but in *sertorius* the central spot became still narrower along veins 4 and 6 and, at the same time becoming angular along vein 5. I cannot consider this character otherwise than apomorphous. In Fig. 37 it is represented by the number 9b.

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Fig. 37. Supposed evolution in the *Spialia sertorius* species group. The numbers indicate characters as indicated in the text. O = plesiomorphic condition, ● = apomorphous condition
The most advanced development of the central spot is found in *sertorius ali*, where the spot is projected towards termen and base, while also the submarginal spots are stretched out. This situation has been represented in Fig. 37 by the number 9c.

(10). Colour of the spots on the upperside. In all *Spialia* species this colour is white, but in *sertorius therapne* and in the summer brood of *sertorius ali* it is yellow. Undoubtedly the yellow colour is an apomorphous character and there is no apparent need for considering the yellow colour to have evolved independently in *sertorius therapne* and *sertorius ali*. It would, however, be very elucidating if the genetic background of this character was known, as apparently ecological factors influence the expression of the character (at least in *sertorius ali*).

(11). Submarginal markings on the upperside. The development of the submarginal markings is subject to much variation in superspecies *sertorius*. Though the genetic background is rather obscure, the expression of this character appears to be determined more ecologically than geographically, see under *sertorius sertorius* and *orbifer orbifer*. However, the whole Asiatic range of *orbifer* east of the Caspian Sea is inhabited by populations in which the submarginal spots are faint or absent, thus indicating that these populations are apparently incapable of developing well-marked submarginal spots. As in almost all *Spialia* species the submarginal spots are well-developed, the absence of these spots in some populations of a single species appears to be an apomorphous character.

(12). Number of broods per year. In superspecies *sertorius* the usual number of broods per year is two, though one brood may be more or less suppressed by ecological factors (mainly at higher elevations in the mountains). However, in spite of the large ecological diversities in Asia, the populations of *orbifer* east of the Caspian Sea appear to be single-brooded. Unless we assume that the double-brooded condition arose independently in *sertorius* and in the *orbifer* populations west of the Caspian Sea, the single-brooded condition must be considered apomorphous. In Fig. 37 this situation is represented by number 12a.

Very probably *sertorius therapne* also is single-brooded. In this case, too, it must be an apomorphous condition, that evidently arose independently of the development in Asia (Fig. 37: 12b).

2. Geographic history.

It is striking that there is only a single *Spialia* species in the Oriental region (*galba*) and, apart from the eremian *phlomidis* group only two *Spialia* species (united in superspecies *sertorius*) in the Palaearctic region, while there are many species in the Ethiopian region. Together with the supposed evolutionary history as expressed in Fig. 37, this makes it probable that *galba* and superspecies *sertorius* have an Ethiopian origin. Evidently, superspecies *sertorius* is the older offshoot. As the ancestor of superspecies *sertorius* appears to have been the only one that successfully colonized the Palaearctic, the eremian zone between the Palaearctic and Ethiopian regions must have been a serious barrier since long, even when it was much narrower than at present. In this connection, it is interesting that the eremian zone not only did not function as a barrier for the ancestor of the *phlomidis* group, but even became its habitat.

Possibly the widening of the eremian zone quickened and intensified the geographic isolation of the ancestor of superspecies *sertorius*. The evolutionary history and the little
variation in Asia east of the Caspian Sea show that this part of the range was colonized rather recently. Thus, the ancestor of superspecies *sertorius* inhabited the Mediterranean and there it became differentiated in *sertorius* and *orbifer*. The distribution of these (semi-)species shows the apparent cause of the differentiation, viz., geographic isolation in a western (*sertorius*) and an eastern (*orbifer*) Mediterranean refugium during a Glacial Period. The occurrence of *orbifer* in Sicily indicates that *sertorius* most probably originated in Spain, in a later time invading Italy where *orbifer* had become extinct during the preceding Glacial Period (possibly except in southern Calabria).

The close relationship between *sertorius therapne* and *sertorius ali* is somewhat puzzling as their distribution areas lie far apart, while the intermediate area is populated by *sertorius sertorius*. If we have interpreted the facts correctly, the following explanation may be an exact reconstruction of the history. At a moment that the red colour of the underside of the hind wing had developed to a certain degree, but probably not yet to the bright red of some recent populations of *sertorius sertorius*, in the western-most populations the white spots of the upperside became yellowish in the summer brood, while in more eastern populations (Italy) the spots remained white. Possibly this differentiation was initiated and influenced by a geographic discontinuity caused by a Glacial Period, but this is, of course, not necessary. A Glacial Period destroyed the greater part of the western-most populations and west of Italy the species survived in isolated areas only, viz., N. Africa, Corsica and Sardinia. As they are surrounded by water, these areas could not have much importance for the expansion of the species in an Interglacial Period and so the intermediate region became populated from another refugium (Italy). By inbreeding and other factors, the populations of Corsica and Sardinia became single-brooded without losing the yellow colour of the spots on the upperside: *sertorius therapne* is, as it were, the summer brood of *sertorius ali*, without producing a spring brood. Isolated in N. Africa *sertorius ali*, or rather its precursor, developed the peculiar markings on the underside of the hind wing, but the yellow spots remained the characteristic of the second brood.

There are two other explanations possible for the discontinuous distribution of the yellow spots: (1) the Iberian populations were not destroyed, but they lost again the newly developed character of the yellow spots, and (2) the yellow spots arose independently in *sertorius therapne* and *sertorius ali*. Both explanations appear to me less probable than the one given first.

The great diversity of *sertorius* in Spain may be an argument for the assumption that Spain was colonized from the east by a multiple invasion so that its genetic variability did not yet attain an equilibrious condition. In this way, possible remnants of populations with yellow spots in the second brood could have been trodden under foot.

In the meantime, *orbifer* invaded Asia. The lack of data from E. Russia and W. Siberia makes it impossible to decide about the route: north or south along the Caspian Sea. The small degree of variation over the large Asiatic range is surprising. It can be the result of a rapid expansion. However, the differentiation between *orbifer lugens* and *orbifer carnea* seems the result of geographic isolations in glacial refugia, so the presence of *orbifer* east of the Caspian Sea must date from the last Interglacial or earlier. Therefore, if the small amount of variation is the result of a rapid expansion, it must have been *orbifer lugens* that expanded its range rapidly from a glacial refugium. In this connection it can have been advantageous, that *orbifer lugens* is single-brooded, giving it the highest survival rate in the extreme continental climate.
The location of the refugium of *orbifer carnea* is not difficult, as this subspecies evidently did not extend its refugial range very much. So it must have survived the last Glacial Period in the Afghan refugium (cf. Gross, 1961; De Lattin, 1967). For *orbifer lugens* it is much more difficult to indicate a glacial refugium. From its present distribution we may conclude that it did not occur south of the Hwang-Ho and that the Mongolian-Siberian refugia are less probable for *orbifer lugens* (species extending from these refugia usually have another distribution pattern). So the Turkestanian and Manchurian refugia are considered for glacial refugia of *orbifer lugens*. The former seems the most probable, as otherwise *orbifer lugens* would already have colonized the whole of its present range before the Last Glacial. In that case, we would have expected a further differentiation of the species in Asia.

The differentiation between *orbifer orbifer* and *orbifer bilaris* is undoubtedly young, not older than since the Last Glacial. Presumably, *o. orbifer* originated in a refugium in the Balkans and W. Turkey, while *orbifer bilaris* did so in Syria/Iran. See, however, the note under ssp. *bilaris* in Chapter 4.

Summarizing, the geographic history of superspecies *sertorius* may be represented as follows.

(1). A northern branch of an Ethiopian species became isolated in the Mediterranean.

(2). Forced by advancing deterioration of the climate during a Glacial Period, the Mediterranean population became divided into a western and a more eastern group giving rise to *sertorius* and *orbifer*, respectively.

(3). During a following Glacial Period, *orbifer* died out in Italy, but could survive in Sicily. In the next Interglacial *orbifer* did not succeed in regaining the lost Italian territory, but was replaced there by *sertorius*. It is interesting to note, that the isolation of *orbifer* in Sicily did not lead to the development of a recognizable differentiation.

(4). In the western populations of *sertorius* the spots became yellow in the summer brood. A following Glacial Period destroyed all or almost all *sertorius* populations in Spain. The character of the yellow spots could survive in Corsica-Sardinia and NW. Africa only.

(5). The “empty” Iberian peninsula was invaded at least once and probably twice or more times by *sertorius* from Italy, resulting in much variation, that is partly locally determined.

(6). In the meantime, *orbifer* invaded Asia east of the Caspian Sea, where it became single-brooded during isolation in a glacial refugium, possibly in Turkestan. After extending its range during an Interglacial, the Central Asiatic population was driven back to glacial refugia during a following Glacial, in Afghanistan (*orbifer carnea*) and possibly in Turkestan (*orbifer lugens*).

(7). In the eastern Mediterranean a differentiation took place between *orbifer orbifer* and *orbifer bilaris* in glacial refugia in the Balkans and W. Turkey and in Syria/Iran, respectively.

(8). After the Last Glacial *sertorius sertorius* extended its range from Italy and presumably also from Spain to the north and the east. In Central Europe it encountered *orbifer*, which advanced from its Balkan refugium to the north and west. The greatest extension of the range was made in Asia by *orbifer lugens* that from its presumably Turkestanian refugium colonized Asia as far as the Amur region and NE. China.

The geographic history outlined above clearly shows the impact of the Glacial Periods
on the development of the superspecies *sertorius*. It is, however, difficult to date the various geographic isolations that must have taken place, as the influence of the different phases of the Glacial Periods are still little understood. Possibly various phases lasted too briefly to have much influence. But even if we claim a whole Glacial Period for each of the supposed geographic isolations, it is still obvious, that the entire development of superspecies *sertorius* took place during the Pleistocene. In other words, the superspecies *Spialia sertorius* originated as a result of the climatic fluctuations of the Pleistocene.

A few words must be said on an earlier hypothesis on a part of the geographic history of the superspecies *sertorius*. To explain the occurrence of species in islands authors have often projected land connections between islands and continents. Even if these connections are geologically demonstrable, we cannot be sure of the use the species made of it. An author who often used former land connections for explaining butterfly distribution in Italy, is Verity (1940). He considered the occurrence of *orbifer* in Sicily the result of the presence of a land connection from Greece through Calabria and Sicily to Tunisia in the Miocene. Apart from the question whether the connection existed in that form, there are the following objections against this explanation:

1. It does not explain the presence of *sertorius* instead of *orbifer* in Calabria.
2. It does not explain, why it is not *sertorius ali* that occurs in Sicily.
3. The Miocene is much too long ago to explain the recent differentiation at the subspecific or semispecific level.

According to Verity, *sertorius ali* is “la forma più primitiva”, from which *sertorius sertorius, sertorius therapne* and *orbifer* originated directly, but in different periods. In this hypothesis *orbifer* is a “trasformazione antichissima”, *sertorius sertorius* originated “fin dal Miocene” and *sertorius therapne* is a “derivazione recente”. Unfortunately, the only argument given by Verity is the shape of the spots on the underside of the hind wing; this argument is far from being convincing. If *orbifer* invaded Sicily in the Miocene, its differentiation from *sertorius ali* must have taken place earlier. It is quite incredible, that a differentiation originating so far back in the Tertiary could maintain itself rather undisturbed in a region that underwent enormous ecological changes. Reasoning in the way of Verity and various other authors, who neglect the overwhelming effect of the Pleistocene Glacial Periods on the differentiation and distribution of the species and forget that the Miocene ended some 12 million years ago (i.e. 12 times as long ago as the beginning of the Pleistocene), would lead to the assumption that the Hesperiidae originated in the beginning of the Tertiary or even earlier and that the Lepidoptera originated tens of millions of years before there were flowers, to suck honey from.

Summarizing, the explanation given by Verity does not explain anything. Apparently the presumption that butterflies cannot cross stretches of sea, is incorrect. This is also demonstrated by the discovery of *sertorius sertorius* in Corsica. This subspecies apparently reached Corsica in recent times, without the help of a land bridge. Moreover, Moreau (1952), summarizing the palaeogeography of Africa, did not mention a Greco-Tunisian land bridge in the Miocene, but only a Sicilo-Tunisian one in the Pliocene. This is much more in accordance with our hypothesis, as it places the evolution of superspecies *sertorius* after the severing of the Sicilo-Tunisian land bridge, i.e. entirely in the Pleistocene. Otherwise, *sertorius ali* would occur in Sicily, or *orbifer* in NW Africa.

Palaearctic species ultimately originating from Ethiopian species appear to be rare.
Their scarcity illustrates the effectiveness of the desert belt (partly in combination with the Mediterranean) as a barrier, though the width of this belt has varied much. Among the Palaearctic Hesperiidae the two Ge Genes species possibly have an Ethiopian ancestry, but they are much more confined to a dry, steppe-like habitat than Spialia sertorius and orbifer.

Undoubtedly other examples can be found among the Palaearctic Lepidoptera, but I do not know of such cases from the literature. Professor Dr. K. H. Voous kindly informed me that a comparable case exists among birds, viz., the Collared Turtle Dove, Streptopelia decaocto, of the roseogrisea/capensis group. But at least part of the extension of this species into the Palaearctic is very young, not older than some centuries.


1. Four species and one superspecies, consisting of two (semi)species, of Spialia, have been recognized in the Palaearctic Region. They can be assigned to two species groups, viz. the pb lomidis group and the sertorius group. The phylogenetic relationship between these groups has not been discussed in this paper, for an examination of such a relationship a revision of the Ethiopian Spialia species is necessary.

2. The pb lomidis group (four species) is confined to the eremian parts of the southern and central Palaearctic. Phylogenetically it is directly related to the Ethiopian species Spialia spio.

3. The sertorius group has a very wide distribution. In the Palaearctic, where it comprises a superspecies with two (semi)species (sertorius and orbifer), it occurs from the Atlantic to the Amur region and China. An Ethiopian (m afa) and an Oriental species (galba) must also be assigned to this species group.

4. By the application of a subspecies definition that uses geographic isolation (at present or formerly) as criterion, several subspecies distinguished by previous authors have been assigned to clinal (local) and nongenetic ecophenotypic variation.

5. The theoretical basis for the arrangement of the species and subspecies adopted in this paper is the discussion on the evolutionary and geographic history. Several characters have been examined as for their apomorphous or plesiomorphous conditions.

6. The pb lomidis group possibly has an Ethiopian ancestry. It developed in a recent time, probably not before the Pleistocene, in the eremian parts of the Palaearctic. The history of the group is obscured by lack of data.

7. The superspecies sertorius is the Palaearctic off-shoot of an Ethiopian ancestor which also gave rise to an Oriental representative of the sertorius group. Superspecies sertorius originated in the Mediterranean as a result of the Pleistocene climatic changes. East Asia was probably reached only in postglacial times, from Turkestan.
7. References


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Postscript

After having sent this paper to the printers', I came across a recent article by L. G. Higgins (J. Ent. (B) 43 (1): 83—87) on a new subspecies of Spialia phlomidis from the Lebanon, which he named S. phlomidis kiki. Evidently, this name is a junior synonym of Spialia phlomidis hermona Evans.

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