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REVISION OF THE *PYRGUS ALPINUS* GROUP (LEPIDOPTERA, HESPERIIDAE), WITH NOTES ON PHYLOGENY AND CHARACTER DISPLACEMENT

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With 21 text-figures and two plates

ABSTRACT

Three species can be recognized in the *Pyrgus alpinus* group, viz., *alpinus*, *darwazicus* and *cashmirensis*. They show an interesting geographic variation, so that a subspecies of one species can be very similar to a subspecies of another species, though other subspecies are quite different. The subspecies recognized are described and illustrated. Two subspecies are described as new, viz., *Pyrgus darwazicus distinctus* and *Pyrgus cashmirensis pumilus*. Distribution maps and drawings of the male and female genitalia of each species are provided.

Although for various characters plesiomorphous and apomorphous states can be distinguished, it is not possible to make a satisfactory choice between the three possible phylogenetic trees of the group.

An analysis of the geographic variation, in which the variations in size and in wing markings are studied separately, suggests that at least part of the variation is due to character displacement. The evidence for the occurrence of this phenomenon in the species group is examined, and it is shown that in at least two instances character displacement offers a satisfactory explanation of the variation found.

INTRODUCTION

The rank of the taxa within the Central Asian *Pyrgus alpinus* group (characterized by the absence of a costal fold in the male) has been changed several times. At present three species can be recognized, viz., *alpinus* Erschoff, *darwazicus* Groum-Grshimailo, and *cashmirensis* Moore. Much confusion arose from the repeated changes of rank (unfortunately a common feature in butterfly taxonomy), which were caused partly by lack of material, partly by a differential evaluation of known facts. As long as no sympatry of any two of the three species recognized now was known, the rank of the taxa remained largely a matter of opinion, the more so as most authors adhered to a typological species concept. Only in 1975, I could record the

sympatry of *P. alpinus* and *P. darwazicus* (De Jong, 1975a), thus giving a solid basis for the specific distinction of both taxa. However, this statement was based on an *alpinus*-like female found together with males and females of *P. darwazicus* at a locality about 500 km from the nearest known locality of *P. cashmirensis*. At that time females available for genital examination were too scarce to be sure that the differences found were of specific value. It has now turned out that the *alpinus*-like female actually belongs to *P. cashmirensis*. Additional material, particularly collections made by Mr. G. Ebert (Karlsruhe), Prof. Dr. C. Naumann (Bielefeld) and Mr. S. Sakai (Tokyo), has not only revealed actual sympatric occurrence of *P. darwazicus* and *P. cashmirensis* in several places covering an extensive area and a possibly large overlap of the distribution areas of *P. alpinus* and *P. cashmirensis*, but it also provides a better insight in the highly interesting geographic variation of the species concerned. As, moreover, in the yet undescribed female genitalia some characters of taxonomic value could be found, it seems worth-while to give a revision of the group. The revision is based on a study of 685 specimens.

The three species were thought to be quite different in external appearance till Alberti (1952) showed that specimens with the *cashmirensis* type of genitalia externally could look exactly like *P. alpinus*, especially in the part of the distribution area of *P. cashmirensis* closest to the supposed distribution area of *P. alpinus*. This situation suggests a kind of "convergent character displacement" (Grant, 1972). The present study brings evidence of other cases of possible character displacement involving *P. cashmirensis* and *P. darwazicus*. After a taxonomic revision of the species group this kind of variation is discussed in relation to the phylogeny of the group.

The distribution maps are based on examined material, with the addition of some reliable literature records of localities I have not seen material from. I have attempted to list all the literature relating to this species group, and to assign all literature records to the correct taxon. If I have overlooked some references, it is unlikely that they would influence the conclusions arrived at in the present paper.

For placing important material at my disposal I am greatly indebted to the following persons and institutions: H. K. Clench (Carnegie Museum of Natural History, Pittsburgh), Dr. W. Dierl (Zoologische Staatssammlung, München), Dr. J. P. Duffels and W. Hogenes (Instituut voor Taxonomische Zoölogie, Amsterdam), G. Ebert (Landessammlungen für Naturkunde, Karlsruhe), Prof. Dr. C. Naumann (Bielefeld), S. Sakai (Tokyo), A. Tsvetajev (Moscow), R. I. Vane-Wright (British Museum (Natural History), London).

Depositories of material have been abbreviated as follows: BMNH, British

Museum (Natural History), London; CMP, Carnegie Museum of Natural History, Pittsburgh; CN, Coll. C. Naumann, Bielefeld; CS, Coll. S. Sakai, Tokyo; LNK, Landessammlungen für Naturkunde, Karlsruhe; RMNH, Rijksmuseum van Natuurlijke Historie, Leiden; ZMA, Instituut voor Taxonomische Zoölogie (Zoölogisch Museum), Amsterdam; ZSM, Zoologische Staatssammlung, München.

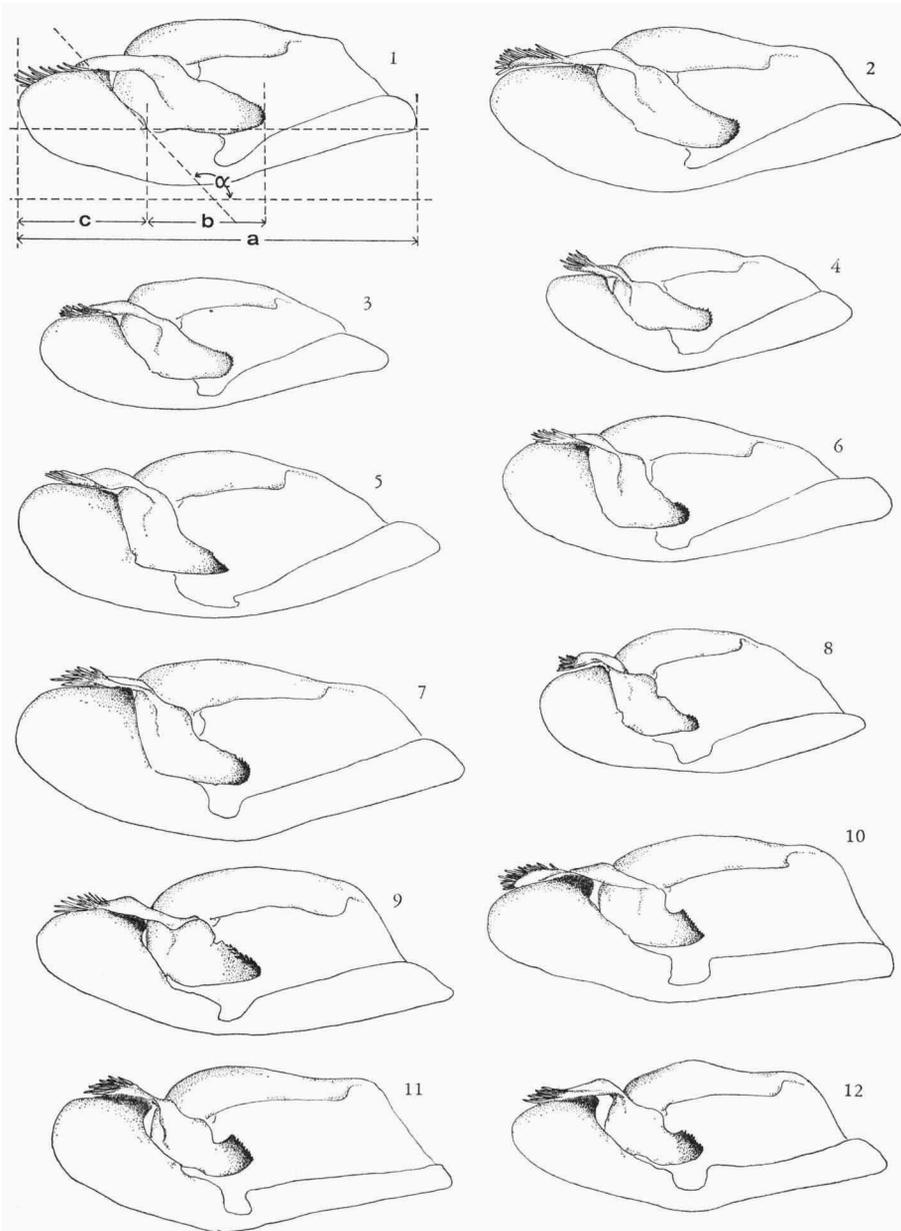
DESCRIPTIONS OF SPECIES AND SUBSPECIES

Pyrgus alpinus (Erschoff)

External characters. — Length of forewing, ♂ (8.9-)10.5-13.5 mm, ♀ 12-14.6 mm. Upperside forewing all median spots, central cell spot and basal spots 10 and 11 present and well-developed; median spot 2 equidistant from median spot 3 and central cell spot, or closer to the latter; no submarginal spots (very rarely some greyish scales replace the spots); greyish dusting in basal part. Upperside hindwing median spots 3-6, sometimes 2-6, rarely 1c-7, and submarginal spots 1c and 2 (subtornal spots) present as white, well-defined spots; usually other submarginal spots more or less indicated by greyish scales; greyish hairs in basal part. Underside forewing spots as on upperside. Underside hindwing spots more or less complete, large, sometimes median spot 2 absent, basal cell spot and basal spot 1c more or less clearly defined, basal spot 7 usually not rounded; ground colour a brownish or yellowish tinge. Females as males.

Diagnostic notes. — *P. alpinus* can be distinguished from the other taxa of the group, except *P. cashmirensis pseudoalpinus*, by the presence of the conspicuous subtornal spots on the upperside of the hindwing. Without genital examination *P. alpinus* cannot be distinguished from *P. cashmirensis pseudoalpinus*.

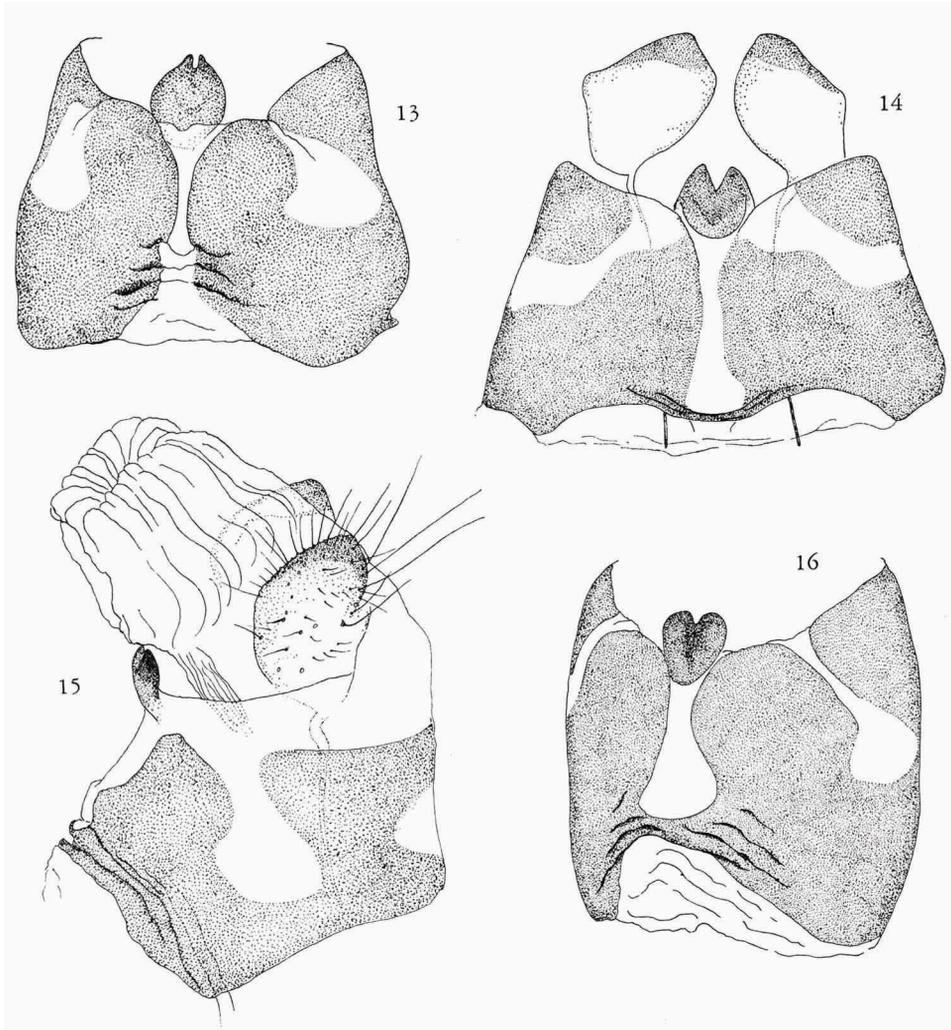
Male genitalia (figs. 1-4). — According to Alberti (1952) the valva of *P. alpinus* differs from that of *P. darwazicus* in being longer and more slender. The impression of slenderness is created by the elongate and oblique cucullus, but in both species the proportion height/length of the valva varies between 0.36 and 0.44. Ventral edge of valva slightly more strongly curved than in *P. darwazicus*, due to the ventrodistally more strongly developed cucullus in the latter. Cucullus relatively long, length 30-35% of total length of valva ($100 \times c/a$, fig. 1); proximal edge oblique, set at an angle of 125-130° to the horizontal plane (α , fig. 1); apex not conspicuously spined. Costa meets cucullus at or before the apex of the latter. Ampulla elongate, spines of dorsal part (stylus) extending to distal edge of cucullus; ventral part (antistylus) elongate but plump, length (28-)34-44% of length of valva



Figs. 1-12. Male genitalia of species of the *Pyrgus alpinus* group; inside of left valva. 1, *P. alpinus alpinus*, Dolon Pass (Tian-Shan); 2, idem; 3, *P. alpinus alichurensis*, Vakhan, Wadi-i-Kol Basi; 4, idem, Caqmaqin, Tergen Quorum; 5, *P. darwazicus darwazicus*, Anzob Pass (Hissar Mts.); 6, idem; 7, *P. darwazicus distinctus*, Kotal-e-Zardeu (Badakhshan); 8, *P. darwazicus celsimontius* (paratype of "*Pyrgus cashmirensis lilliput*"), Anjuman Pass; 9, *P. cashmirensis cashmirensis*, Mt. Kolahoi (Kashmir); 10, *P. cashmirensis pseudoalpinus*, Sarhad (Vakhan); 11, *P. cashmirensis pumilus*, paratype, Khwahan; 12, idem, Tuptschek.

minus cucullus ($100 \times b/a-c$, fig. 1), apex rounded, with short spines reaching beyond the middle of the valva, i.e. closer to the proximal than to the distal end of the valva.

Female genitalia (fig. 13). — Sclerotization of eighth abdominal segment interrupted antevaginally. Genital plate rounded, greatest width about in the



Figs. 13-16. Female genitalia of species of the *Pyrgus alpinus* group; mainly ventral sight of eighth abdominal segment. 13, *P. alpinus alpinus*, Naryn River; 14, *P. cashmirensis pseudoalpinus*, Issik Valley (Vakhan); 15, *P. darwazicus darwazicus*, Anzob Pass (Hissar Mts.), lateral sight, ovipositor slightly extended; 16, *P. darwazicus distinctus*, Khinsch-e-Andarab (Badakhshan).

middle; apical incision shallow, less than 1/6 of total length of plate; apical parts slightly narrowed.

Distribution (fig. 17). — From N. Kashmir through Pamir, Zeravshan and Tian-Shan to Issyk-kul; also known from Siberia and E. Asia. For particulars see under subspecies. As far as can be judged from labelled specimens and literature records the altitudinal range of *P. alpinus* lies between 2500 and 4400 m.

P. alpinus has not yet been found flying together with one of the other species of the group. The earlier record of sympatry with *P. darwazicus* (De Jong, 1975a) turned out to be based on an *alpinus*-like female of *P. cashmirensis* found 500 km from the nearest locality of the latter known at that time. However, in view of the occurrence of *P. alpinus* from Zeravshan to S. Pamir and the occurrence of *P. darwazicus* in the Hissar Mts., Darwaz and W. Pamir, sympatry is highly probable. The same holds for *P. alpinus* and *P. cashmirensis*, as the latter is sympatric with *P. darwazicus* in the area just mentioned and, moreover, occurs in Vakhana and Kashmir where also *P. alpinus* is known from. It is remarkable that in Vakhana *P. alpinus* has only been found in the eastern part (Little Pamir), while *P. cashmirensis* is only known from the central and northern parts (Great Pamir). This may be due to undercollecting rather than to actual vicariance. Of the known localities of *P. alpinus* in N. Kashmir, at least Darkot lies within the area of *P. cashmirensis*.

Geographic variation. — There is variation in size and in the development of the spots, especially of the hindwing, and three subspecies have been recognized previously. New material has shown the situation to be less simple than it seemed to be, because in the southern part of the area, where the small forms occur, there is much variation in size. Possibly the variation could be better described as clinal than as subspecific, but as material from the crucial intervening area, viz., the greater part of Pamir, is still largely lacking, the subspecific division is maintained for the time being.

***Pyrgus alpinus alpinus* (Erschoff)**

Syrichthus alveus var. *alpina* Erschoff, 1874. — Lep. Turkestan: 24; pl. 2 fig. 18. Type-locality: Ktchi Alai (Kokand). Type depository unknown.

Syrichthus alveus v. *alpina*; Crüger, 1874: 393.

Syrichthus alpina; Herz, 1898: 249 (Vilui); Oberthür, 1912: 80.

Scelothrix alpina; Groum-Grshimailo, 1894: 94 (Iskander-kul, Schachsara).

Hesperia alveus var. *alpina*; Kirby, 1877: 830.

Hesperia alpina; Elwes & Edwards, 1897: 160; Staudinger-Rebel, 1901: 97; Mabille, 1904: 82; Reverdin, 1914: 182; 1916: 21; Chapman, 1917: 145; 1918: pl. 9 fig. 1;

Warren, 1926: 163; Gaede, 1931: 317; Forster & Von Rosen, 1940: 815.

Hesperia cashmirensis f. *alpina*; Mabille, 1909: 336.

- Pyrgus alpina*; Plötz, 1884: 10; Groum-Grshimailo, 1890: 501 (pro parte); Shepard, 1935: 400; Alberti, 1952: 79.
Pyrgus alpina alpina; Evans, 1932: 351 (pro parte); 1949: 200 (pro parte).
Pyrgus alpinus; Rühl, 1895: 671; Avinov, 1910: 245 (pro parte); Picard, 1947: 131; Korshunov, 1972: 139.
Pyrgus alpinus alpinus; De Jong, 1972: 48; 1975a: 4.

External characters (pl. 1 figs. 1, 2). — Relatively large, length forewing ♂ (11.2-)11.8-13.5 mm. Spots well-developed on upper- and underside; on upperside of hindwing median spot 2 usually present, sometimes also median spot 1c; on underside of hindwing median spot 4-5 usually extended basad along vein 6, sometimes with a straight inner edge, and median spot 2 present.

Diagnostic notes. — This subspecies is very similar to *P. cashmirensis pseudoalpinus* in external appearance. In the latter the spots on the underside of the hindwing are often still larger than in *P. alpinus alpinus*, and on the upperside of the hindwing median spot 1c is often present, but for a reliable identification, genital examination is indispensable. However, in the area where *P. alpinus alpinus* possibly meets *P. cashmirensis*, the latter is represented by the small ssp. *pumilus* and not by the large ssp. *pseudoalpinus*. Thus size may be indicative of the species in specimens with exact locality data, but it is not sufficient for a reliable identification.

Distribution (fig. 17). — The whole distribution area of the species except South (and possibly East) Pamir and North Kashmir. Known from many localities, but labels often give only region or mountain range (usually omitting altitude) or localities that cannot be found on maps or in gazetteers. Thus, although the species may be widely distributed in the mountainous regions of the old province of Samarkand, only vague indications such as "Samarkand" or "Zeravshan" can be found. The distribution area in Central Asia is probably continuous, as far as the habitat allows. Separated from it *P. alpinus alpinus* occurs in East Asia, according to specimens labelled "Kukunoor" (2 ♂, ZSM), "Ussuri" (1 ♂, ZSM), "Amur" (4 ♂, 1 ♀, BMNH), "Siberia" (1 ♀, BMNH), and "Awatschin Bai, Kamtschatka" (4 ♂, ZSM). When publishing his catalogue of the Hesperidae in the British Museum (Natural History), Evans (1949) apparently did not trust the labels of the East Asian specimens, but in my opinion there are too many specimens from East Asian localities to think of false data. Moreover, there is a literature record from Vilui (N. Siberia) by Herz (1898) that is quite reliable. However, the Altai, casually mentioned as locality of *P. alpinus* by Alberti (1952), may be a misprint for "Alai", as no material or other records seem to be known from the Altai Mountains.

Material examined. — 165 ♂, 66 ♀ (BMNH, CMP, RMNH, ZSM). Localities: Samarkand, Zeravshan, Sultan Hasret Mts., Transalai, Alai,

Ispajran (N. Alai), Djol-boerul (NE. Pamir), Ferghana, Kokand, Margelan, Tura, Naryn River, Fort Naryn, Dolon Pass, Ush Tash (Kashgar), Little Kizil-su, Auli Ata, Arptal, Aksu, Taschrabat, Tog-Tjurae, Alexander Mts., Issyk-kul, Kukunor, Ussuri, Amur, Awatschin Bay (Kamtschatka).

Pyrgus alpinus alichurensis De Jong

Pyrgus alpinus alichurensis De Jong, 1975a. — Zool. Meded. Leiden 49: 6. Type-locality:

Koytezek Pass, S. Alichur Mts. Holotype (♂) in RMNH.

Pyrgus alpina; Groum-Grshimailo, 1890: 501 (pro parte).

Pyrgus alpinus; Avinov, 1910: 245 (pro parte).

Pyrgus alpina alpina; Evans, 1949: 200 (pro parte).

External characters (pl. 1 figs. 3, 4). — Small, length of forewing ♂ (8.9-)10.8-11.8(-12.3) mm. On the upperside spots relatively large and angular, but on the hindwing median spot 1c always and 2 usually absent. On the underside of the hindwing median spot 2 absent, median spot 4-5 usually with a projection towards the base of the wing along vein 6.

Diagnostic notes. — This subspecies differs from ssp. *alpinus* by its small size, and from ssp. *mustagatae* by the relatively large spots on the upperside of the wings and the less reduced spots on the underside of the hindwing. It is smaller than *P. cashmirensis pseudoalpinus*, with which it is probably sympatric (see also the diagnostic notes under ssp. *alpinus*).

Distribution (fig. 17). — Only known from Pamir, Vakhan and N. Kashmir. As far as altitudes have been stated on the labels, the specimens come from 4000-4400 m. Groum-Grshimailo (1890) recorded Col Beik (4400-4600 m, Konjout Mts.) as locality of *P. alpinus*. As this locality is in SE. Pamir, the record may relate to ssp. *alichurensis*. However, as Groum-Grshimailo did not give a description of the specimens, they may also belong to *P. cashmirensis pseudoalpinus*.

Material examined. — 21 ♂ (including holotype), 2 ♀ (BMNH, LNK, RMNH). Localities: Koytezek Pass (S. Alichur Mts.), Wadi-i-Kol Basi, Kotal-e-Toghuz Bash, Tergen Quorum (last three in E. Vakhan), Darkot (N. Gilgit), Misgar (N. Hunza). The specimens from the last locality (BMNH; labelled "Misgah", apparently a misprint for "Misgar") were listed under ssp. *mustagatae* by De Jong (1972), but since ssp. *alichurensis* was distinguished the rather worn specimens seem to fit better this subspecies.

Pyrgus alpinus mustagatae Alberti

Pyrgus alpina mustagatae Alberti, 1952. — Z. Lepid. 2: 80. Type-locality: Muztagh Ata.

Holotype (♂) in Coll. Alberti (Göttingen).

External characters. — Small, about same size as ssp. *alichurensis*, length forewing ♂ 11 mm. On upperside spots as in ssp. *alpinus*. On underside of

hindwing spots reduced, median spot 7 wider than other median spots, 4-5 without projection towards base, according to original description median spots 1c-3 absent (“... die mediane Binde schon im Diskus endet...”).

Diagnostic notes. — The distinction of the three subspecies of *P. alpinus* is rather subtle, and its justification uncertain by lack of material. I doubt whether the characters mentioned by Alberti for ssp. *mustagatae* are really constant.

Distribution (fig. 17). — Only known from the Muztagh Ata, a very high mountain in the Chinese part of Pamir. Altitude not specified.

Material examined. — 1 ♂, 1 ♀, paratypes (ZSM).

***Pyrgus darwazicus* Groum-Grshimailo**

External characters. — Length of forewing, ♂ 9.8-13.4 mm, ♀ 11.3-14.2 mm. It was stated by Groum-Grshimailo (1890), Reverdin (1933), and Alberti (1952) that the female is remarkably larger than the male, but these observations were based on scarce material. Although on the average the female is larger than the male, the difference is usually rather slight and there is some overlap. Upperside forewing all median spots present, reduced or almost entirely absent; median spot 2 about equidistant from median spot 3 and central cell spot, or slightly closer to the latter; central cell spot and basal spot 10 usually present, basal spot 11 and discoidal spot may be present, but never conspicuous; submarginal spots absent or indicated by grey scales. Upperside hindwing almost completely immaculate dark brown or spotted, median and submarginal spots may all be present, but always vaguely outlined and never clear-white; submarginal spots 1c and 2 (subtornal spots) never conspicuously better developed than other submarginal spots. Underside forewing spotting as upperside, spots slightly larger. Underside hindwing median spots complete (1c-7) or reduced in number (4-7), usually separated by ground colour along the veins; submarginal spots variable, almost absent to small but complete; basal spot 7 small and inconspicuous or obvious, rounded; ground colour varying from a dark brown-grey to yellowish grey, in females usually of a lighter shade.

Diagnostic notes. — *P. darwazicus* can always be distinguished from *P. alpinus* by the subtornal spots on the upperside of the hindwing, which are never conspicuous and sometimes absent in *P. darwazicus*, and always conspicuous in *P. alpinus*. For differences with *P. cashmirensis*, see under subspecies.

Male genitalia (figs. 5-8). — Similar to those of *P. alpinus*, differing in some details of the valva. Cucullus shorter and more rounded than in *P. alpinus*, length of cucullus 25-30(-33)% of length of valva ($100 \times c/a$, fig.

1); apical spines about as in *P. alpinus*, not as strongly developed as in *P. cashmirensis*; proximal edge less oblique than in the other species of the group, set in a angle of 101-118° to the horizontal plane (α , fig. 1). Ampulla shorter than in *P. alpinus*; dorsal part (stylus) not reaching distal edge of cucullus; ventral part (antistylus) variously shaped, often more or less triangular, but it may be very similar to the structure found in *P. alpinus*, only shorter, its relative length being 27-35(-37)% of the length of the valva minus cucullus ($100 \times b/a-c$, fig. 1), and its apex about halfway the length of the valva. The remark by Alberti (1952) that the more or less triangular shape of the antistylus with its acute apex is the essential feature of *P. darwazicus*, was premature, being based on only two specimens. On the basis of the shape of the antistylus alone a reliable identification is often impossible. The dorsal edge of the costa meets the cucullus about at the apex of the latter. The ventral edge of the valva is, on the average, less strongly curved than in *P. alpinus*, due to the greater ventrodistal development of the cucullus.

Female genitalia (figs. 15, 16). — Sclerotization of eighth abdominal segment narrowly continuous antevaginally. In this character *P. darwazicus* resembles *P. cashmirensis*. In the latter the antevaginal sclerotization seems to be narrower, but this may be subject to variation and is moreover difficult to measure. Genital plate widest above middle; apical incision shallow, about 1/5-1/6 of total length of plate; apical parts rounded.

Distribution (fig. 18). — From the Koh-i-Baba Mts. in C. Afghanistan to the Hissar Mts. (Gissarskiy Khrebet) and NW. Pamir; 2300-4300 m. Sympatric with *P. cashmirensis* over the greater part of the distribution area.

Geographic variation. — In general the northern populations (Hissar Mts. NW. Pamir) are dark above and below, with reduced spots; the central populations (N. Afghanistan) are about as large as the northern populations, but well-spotted; the southern populations (S. Badakhshan) are small, with spotting more or less intermediate. In this way three rather well-defined groups of populations can be recognized at the moment; they will be treated here as subspecies. It is not impossible that additional material from intermediate localities will reveal some sort of clinal variation, but the present material does not yet demonstrate this clearly.

The variation is not simply an altitudinal one, in the sense that small and/or dark specimens would occur at higher altitudes than larger and better marked specimens, as all subspecies have been found at the same altitudes.

***Pyrgus darwazicus darwazicus* Groum-Grshimailo**

Pyrgus alpina var. *darwazica* Groum-Grshimailo, 1890. — In: Romanoff, Mém. Lépid. 4: 501; pl. 21 fig. 5. Type-locality: Tuptschek (Darwaz Mts.). Holotype (δ) in BMNH.

- Scelothrix alpina* var. *darwazica*; Groum-Grshimailo, 1894: 94 (Mura Pass).
Syrichthus alpina darwazica; Oberthür, 1912: 80.
Hesperia alpina darwazica; Staudinger-Rebel, 1901: 97; Warren, 1926: 163; Gaede, 1931: 317.
Hesperia alpina alpina; Evans, 1932: 351 (pro parte).
Hesperia alpina submurina Reverdin, 1933. — Mitt. schweiz. ent. Ges. 15: 498. Type-locality: Dombratschi (S. Buchar). Holotype (♂) in ZSM. Synonymy by Alberti (1952).
Pyrgus alpinus var. *darwazica*; Rühl, 1895: 671.
Pyrgus alpina darwazica; Shepard, 1935: 401; Evans, 1949: 200.
Pyrgus alpinus darwazica (sic!); Korshunov, 1972: 139.
Pyrgus darwazicus; Von Rosen, 1921: 99 (pro parte).
Pyrgus darwazica; Alberti, 1952: 80.
Pyrgus darwazicus darwazicus; De Jong, 1972: 51; 1975a: 6-7.

External characters (pl. 1 figs. 5, 6). — Length of forewing, ♂ 11.4-13.2 mm, ♀ 12.8-14 mm. Upperside forewing spots variable, all median spots, central cell spot and basal spot 10 may be present, but always small and reduced, and in some specimens only traces of the subapical spots (median spots 6-8) are left, the wings thus being almost immaculate black-brown; no lighter superscaling near base, no traces of submarginal spots. Upperside hindwing spots, if present, only faintly visible, at most median spots 3-6 and submarginal spots 1c and 2 (very rarely some more) visible. Underside forewing spotting better developed than on upperside; median spot 2 usually closer to the central cell spot than to median spot 3. Underside hindwing spots reduced; in the male usually only median spots 4-7, and sometimes basal spot 7 visible, vaguely outlined, more or less obscured by the dark greenish or brownish grey ground colour that also obscures the submarginal spots; in the female the spots are better developed and the ground colour is of a lighter, yellow shade.

Diagnostic notes. — This subspecies is characterized by the dark upper- and undersides of the wings, caused by the reduction of the spots and darkening of the ground colour of the underside of the hindwing. Even in the darkest specimens of ssp. *distinctus*, which on the upperside are rather similar to ssp. *darwazicus*, the spots on the underside of the hindwing are far better developed.

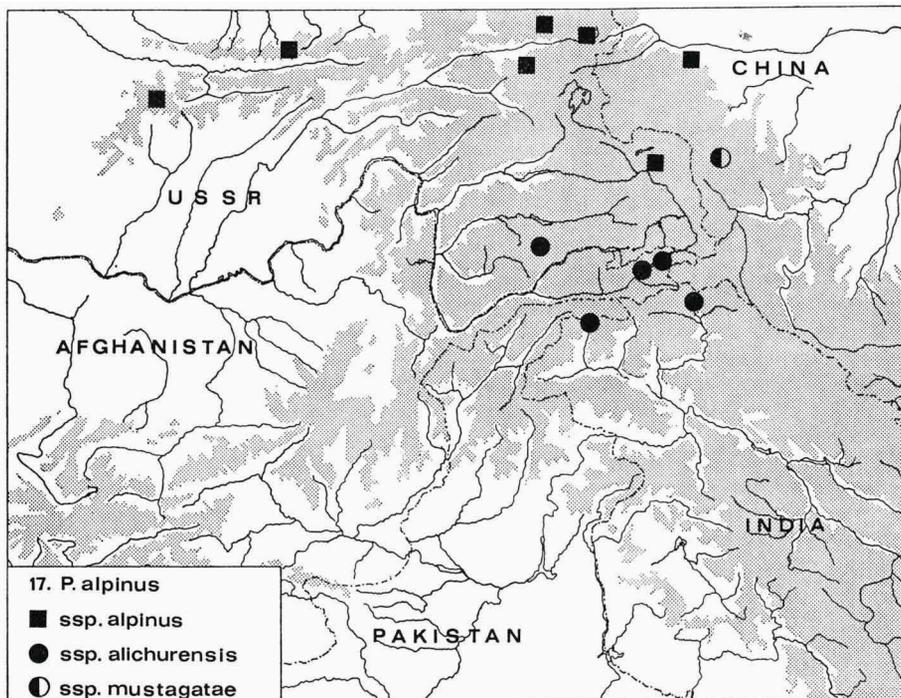
Distribution (fig. 18). — Confined to the northern part of the distribution area of *P. darwazicus*, from the Hissar Mts. (Gissarskiy Khrebet) north of Dushanbe, eastwards to western Pamir (Darwaz, Alai, Transalai). Specimens labelled "Samarkand" probably originate from the Hissar Mts. As the localities "Alai" and "Transalai" are little exact, they have not been indicated on the map. The subspecies has been found flying together with *P. cashmi-rensium pumilus*, from which it can be distinguished by larger size and more reduced spotting.

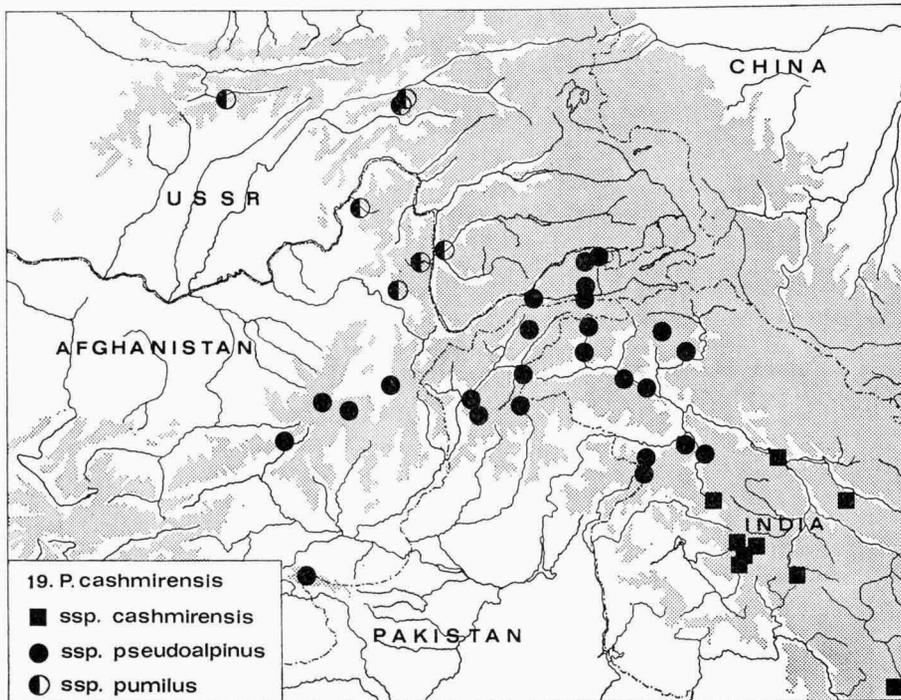
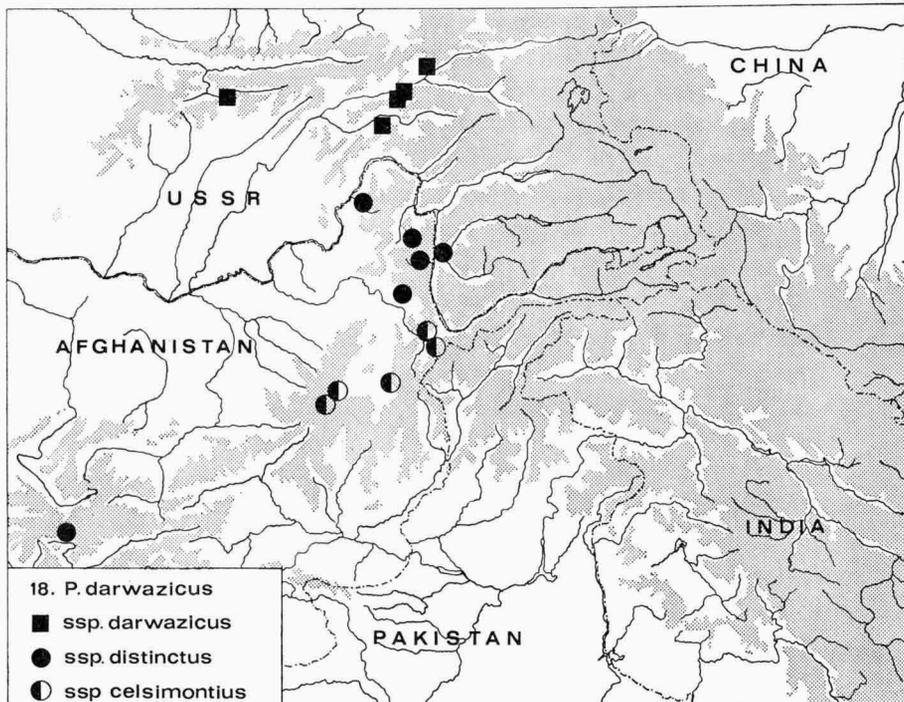
Material examined. — 21 ♂, 9 ♀, including holotypes of "*Pyrgus alpina* var. *darwazica* Groum-Grshimailo" and of "*Hesperia alpina submurina* Reverdin" (BMNH, RMNH, ZSM). Localities: Anzob Pass, Tuptschek, Jaschil-kul (near Tuptschek, not the large lake with the same name further east in Pamir), Kaschkasu, Borolmos glacier, Dombratschi, Alai, Transalai.

***Pyrgus darwazicus distinctus* subsp. nov.**

Pyrgus darwazicus celsimontius; De Jong, 1972: 51 (pro parte; Shiva L.); 1975a: 7.

External characters (pl. 1 figs. 7, 8). — Length of forewing, ♂ 11.8-13.4 mm, ♀ 13.3-14.2 mm. Upperside forewing all median spots and central cell spot well-developed, basal spot 10 always, 11 often present; submarginal spots often indicated by greyish scales; basal part of wing usually covered with greyish scales and hairs; median spot about equidistant from median spot 3 and central cell spot; discoidal spot usually visible as a fine greyish line. Upperside hindwing, of median spots at least 3-6, often 1c or 2 to 6 or 7 well visible; of submarginal spots at least 1c and 2, but often 1c-6 indicated by greyish scales, and sometimes rather well-defined; basal part of wing with greyish hairs. Underside forewing spots as on upperside, but slightly better





Figs. 17-19. Localities of *Pyrgus alpinus*, *darwazicus* and *cashmirensis* in Central Asia. *P. alpinus* and *cashmirensis* are also distributed outside the area of the maps, see text.

developed. Underside hindwing all median spots (1c-7) present and well-defined, separated by ground colour along veins, sometimes spots 1c and/or 2 reduced; inner edge of spot 4-5 straight or extended basad along vein 6; submarginal spots complete; basal spot in space 7 sharply defined, rounded, white; ground colour yellowish or brownish grey, whitish or greyish along termen. Female similar to male, or ground colour of underside of hindwing more yellowish.

Diagnostic notes. — This is the most strongly marked subspecies of *P. darwazicus*. The difference between ssp. *distinctus* and ssp. *darwazicus*, which are about equally large, is obvious on the upper- as well as on the underside, but especially on the underside of the hindwing, where in ssp. *darwazicus* the ground colour is darker and the spots reduced in size and number. The underside of the hindwing of ssp. *distinctus*, with the rounded basal spot 7, the median spots separated by the veins and the often yellowish grey ground colour, strongly reminds of the underside of the hindwing in the alpine populations of *Pyrgus serratulae* Rambur in the Alps. In the rather well-marked ssp. *celsimontius* the spots are, on the average, slightly smaller than in ssp. *distinctus*, but the most obvious difference between these subspecies is found in the size.

Ssp. *distinctus* flies sympatrically with *P. cashmirensis pumilus* over the whole of its distribution area. These taxa may look rather similar. Apart from the difference in size (ssp. *pumilus* is usually smaller), they can be separated by the more extensive and whiter spots on the underside of the hindwing in ssp. *pumilus*, with the median spots conjoined, median spot 1c always well-developed, even if spot 2 is absent, median spot 4-5 always obviously extended basad along vein 6, and basal spot 7 less rounded. These differences may seem subtle, but with some experience one can tell most specimens apart with certainty using only external characters. In cases of uncertainty a short glance at the inside of the valva is sufficient for identification.

Distribution (fig. 18). — Confined to the northern-most parts of Afghanistan and adjacent part of western Pamir. In Coll. Naumann there is a male entirely agreeing with this subspecies (see fig. 21), but originating from "Prov. Bamian, vic. Pandjao". This is remarkable as between Panjao and northern Badakhshan (where the other specimens come from) ssp. *celsimontius* flies. For the time being the Panjao specimen has been recorded on the map as belonging to ssp. *distinctus*. More material is needed to clear up this situation. The occurrence of a large form south of the area of ssp. *celsimontius* is discussed below, under character displacement.

Material examined. — Holotype ♂, Khorog (Tadzhikistan), 2700 m,

25.VII.1965, leg. A. Tsvetajev (RMNH). Paratypes: 3 ♂, same data as holotype (RMNH); 19 ♂, 4 ♀, Kotal-e-Zardeu (15 km N of Baharak), 3000-3200 m, 29-30.VI.1971, leg. Ebert & Naumann (LNK); 1 ♂, 1 ♀, idem, but 1-4.VII.1971, leg. Naumann (CN). Further material: 9 ♂, 1 ♀, Khwahan (Nasher, Kotal-e-Kamkhas, Pari Kham), 2300-3500 m (CN); 17 ♂, 4 ♀, Kotal-e-Zardeu (15 km N of Baharak), 3000-3200 m (LNK); 1 ♂, 1 ♀, Khinsch-e-Andarab, 3500-4000 m (ZSM); 1 ♀, Shiva Mts, 2600 m (LNK); 1 ♂, Panjao, 2300 m (CN).

***Pyrgus darwazicus celsimontius* Kauffmann**

Pyrgus darwazica celsimontia Kauffmann, 1952. — Z. Lepid. 2: 85-86, figs. 3-4. Type-locality: Sebak Valley (Badakhshan). Holotype (♀) in ZSM. Alberti (1952) incorrectly stated the holotype to be a male.

Pyrgus cashmirensis lilliput Wyatt et Omoto, 1966. — Entomops 1966: 195-196. Type-locality: Bala Quran (Anjuman Valley). Holotype (♂) in LNK.

Pyrgus darwazicus lilliput; De Jong 1972: 51; 1975a: 7.

External characters (pl. 2 figs. 9, 10). — Small, length of forewing, ♂ 9.8-11.2 mm, ♀ 11.3-12.0 mm. According to Alberti (1952) the wing-span of this subspecies is ♂ 24-26 mm, ♀ 29 mm. It does not at all agree with the type specimens examined by me (holotype, allotype, paratype). The holotype, stated by Alberti to be a male, but turning out to be a female, has a wing span of 23 mm (length of forewing 12 mm), and the paratype (♂) 20 mm (length of forewing 10.7 mm). The condition of the allotype is too bad for reliable measurements, the right forewing being absent and the left forewing crumpled. According to the original description ssp. *celsimontius* is "wesentlich kleiner als *darwazica*", but I have not seen any female of ssp. *darwazicus* with a wing span of more than 28.5 mm. Thus some errors must have crept in the original description and the statements by Alberti. Realizing this, the synonymy of *P. darwazicus celsimontius* and *P. cashmirensis lilliput* becomes apparent, if one knows that the latter has the *darwazicus* type of genitalia (see De Jong, 1972).

Upperside forewing all median spots present, usually well-developed, but in a few specimens small and spot 4 almost invisible; central cell spot well-developed; median spot 2 usually closer to the central cell spot than to median spot 3, sometimes equidistant; basal spot in space 10 (over central cell spot) and sometimes in space 11, present: no submarginal spots; discoidal spot absent or indicated by a few greyish scales. Upperside hindwing median spots present in spaces 3-6, sometimes also in spaces 2 and 7, rarely reduced to a single spot in spaces 4-5; submarginal spots variable, usually well visible in a more or less complete row, and then all spots equally well-developed. Underside forewing spotting as upperside. Underside hindwing median spots

variable, often only present in spaces 4-7, but sometimes also in spaces 1c and 3, very rarely in space 2; median spot in spaces 4-5 relatively narrow, not wider than long (length is distance from vein 4 to vein 6), inner edge straight or slightly sloping basad along vein 6; basal spot in space 7 small, round; submarginal spots indistinct, more or less overshadowed by the ground colour, those in spaces 1c, 2 and 6 usually most distinct; ground colour dark greyish brown, often greyish along termen. Female as male, but ground colour of hindwing underside of a lighter shade.

Diagnostic notes. — The most salient feature of this subspecies is its small size, being distinctly smaller than both ssp. *darwazicus* and ssp. *distinctus*. It may be rather similar to *P. cashmirensis pumilus*, but apart from the difference in the genitalia the latter has usually larger and more distinct spots above as well as below: the submarginal spots in spaces 1c and 2 on the upperside of the hindwing are better developed than the other submarginal spots (rather like in *P. alpinus*); the median spot in spaces 4-5 on the underside of the hindwing is wider, with a distinct basad projection along vein 6; and the ground colour of the underside of the hindwing is less greyish, more greenish.

Distribution (fig. 18). — Confined to Afghanistan, where it occupies the southern-most part of the distribution area of the species, from the Anjuman Pass to the Sebak Valley (see, however, the locality Panjao under ssp. *distinctus*). Sympatric with *P. cashmirensis pseudoalpinus* at Anjuman Pass and Koh-i-Munjan.

Material examined. — 32 ♂, 8 ♀, including holotype and paratypes of both "*Pyrgus darwazica celsimontia* Kauffmann" and "*Pyrgus cashmirensis lilliput* Wyatt et Omoto" (CN, CS, LNK, RMNH, ZSM). Localities: Anjuman Pass, Bala Quran, Anjuman Valley, Koh-i-Munjan, Nuksan Pass, Sebak Valley.

***Pyrgus cashmirensis* Moore**

External characters. — Length of forewing, ♂ 10.4-14.1 mm, ♀ 11.5-15 mm. Upperside forewing all median spots, central cell spot, and basal spot 10 and often 11 present, no submarginal spots; median spot 2 equidistant from median spot 3 and central cell spot, or close to the latter so that the central cell spot and median spots 1b-c and 2 are in line. Upperside hindwing markings variable, from almost invisible to sharply outlined, white, median and subternal spots. Underside forewing spotting as on upperside. Underside hindwing spots variable in extension, always well contrasting with the greenish or olive brown ground colour.

Diagnostic notes. — *P. cashmirensis* can be similar to both other species of

the group. There is no external character by which *P. cashmirensis* can always be distinguished, and genital examination is sometimes necessary. See also the diagnostic notes under the subspecies.

Male genitalia (figs. 9-12). — General shape of valva as in *P. alpinus*; proportion height/length 0.39-0.45; ventral edge curved as in *P. alpinus*. Cucullus relatively long, 29-34.5% of total length of valva ($100 \times c/a$, fig. 1); proximal edge oblique, in the lower part set at an angle of 125-142° to the horizontal plane (α , fig. 1), in the upper part conspicuously concave; apex thickly set with short spines; dorsal edge flattened or slightly concave. Costa meets cucullus well below the apex of the latter, at some point along its proximal edge. Ampulla rather plump; spines of stylus usually not entirely reaching the distal edge of the cucullus; antistylus relatively short, length 24.7-31.7% of length of valva minus cucullus ($100 \times b/a-c$, fig. 1), with apex not reaching beyond middle of valva, truncated, curving inwards (i.e. to the opposite valva), the almost straight edge serrated with short teeth.

The shape of the ventral part of the ampulla (antistylus), the concave proximal edge of the cucullus, and the thickly spined apex of the cucullus easily distinguish *P. cashmirensis* from the other species of the group. The characters of the cucullus are usually even visible by simple clearing of the tip of the abdomen.

Female genitalia (fig. 14). — Sclerotization of eighth abdominal segment narrowly continuous antevaginally. Genital plate more or less rounded, apical incision relatively wide, V-shaped, about 1/3 of total length of plate.

Distribution (fig. 19). — From Hissar Mts. (Gissarskiy Khrebet) to Central Hindu-Kush, and through Pamir and Kashmir east to Kumaon; Bhutan (discontinuously?). Altitudinal range 2400-4400 m. Sympatric with *P. darwazicus* over a wide area; probably also sympatric with *P. alpinus*.

Geographic variation. — The species is highly variable geographically, and on the basis of the available material the distinction of three well-defined subspecies seems justified. It is interesting to note that one subspecies is similar to *P. alpinus*, and one other to a form of *P. darwazicus*, so that *P. cashmirensis* exhibits the most pronounced variation in the *P. alpinus* group.

***Pyrgus cashmirensis cashmirensis* Moore**

Pyrgus cashmirensis Moore, 1874. — Proc. zool. Soc. London 1874: 274; pl. 42 fig. 7.

Type-locality: Kashmir. Holotype (♂) in BMNH.

Hesperia cashmirensis; Watson, 1893: 65; 1895: 422; Elwes & Edwards, 1897: 160; Mabille, 1904: 82; 1909: 336; Swinhoe, 1912: 96; Hannyngham, 1915: 197; Reverdin, 1916: 21; Warren, 1926: 163; Gaede, 1931: 317.

Syrichthus kashmiriensis (sic!); Elwes, 1888: 293.

Syrichthus cashmirensis; Oberthür, 1912: 80.

Hesperia alpina cashmirensis; Evans, 1912: 1000; 1932: 351.

Hesperia alpina durwazica (sic!); Evans, 1912: 1000.

Pyrgus alpina cashmirensis; Evans, 1949: 200.

Pyrgus cashmirensis; Shepard, 1935: 401; Picard, 1947: 131; Alberti, 1952: 81.

Pyrgus cashmirensis cashmirensis; De Jong, 1972: 49; 1975a: 7.

External characters (pl. 2 figs. 11, 12). — Length of forewing ♂ and ♀ 12.5-13.9 mm. Upperside forewing all median spots, central cell spot and basal spots 10 and 11 present and well-developed; median spot 2 close to the central cell spot, so that median spots 1b-c and 2, and central cell spot are in line; no submarginal spots; no greyish basal dusting. Upperside hindwing without submarginal spots, median spots at most vaguely indicated in spaces 3-6, usually almost invisible. Underside forewing spotting as on upperside. Underside hindwing, all spots large and contrasting well with the greenish brown ground colour. Female similar to male.

Diagnostic notes. — The weak development of the spots on the upperside of the hindwing distinguishes this subspecies from the other taxa of the *P. alpinus* group, except *P. darwazicus darwazicus*. In the latter, however, the spots on the upperside of the forewing and on the underside of the hindwing are much reduced.

Distribution (fig. 19). — Widely distributed from Baltistan (Kashmir) through Ladakh, Lahoul and Kulu to Kumaon; Bhutan. It has not yet been recorded from Nepal, but its occurrence can be expected there.

Material examined. — 127 ♂, 54 ♀, including holotype of "*Pyrgus cashmirensis* Moore" (BMNH, CMP, CS, LNK, RMNH, ZSM). Localities: Burzil Pass, Baltistan, Kashmir, Ladakh, Nunkun, Mt. Kolahoi, Upper Amarnath, Pahalgam, Lidarwat, Sekiwas, Thajiwas Valley, Chandra River, Lahoul, Rohtang Pass, Kulu, Kumaon, Bhutan.

***Pyrgus cashmirensis pseudoalpinus* Alberti**

Pyrgus cashmirensis pseudoalpina Alberti, 1952. — Z. Lepid. 2: 85. Type-locality: Gilgit.

Holotype (♂) in Coll. Alberti (Göttingen).

Hesperia cashmirensis; Leslie & Evans, 1903: 677.

Hesperia alpina; Evans, 1912: 1000; 1927: 162.

Hesperia alpina alpina; Evans, 1932: 351 (pro parte).

Pyrgus alpina alpina; Evans, 1949: 200 (pro parte).

Pyrgus alpinus alpinus; Shirôzu & Saigusa, 1963: 104 (Mochodan-Tikatoki, Tikatoki-Diwan Gal, both in West-Pakistan).

Pyrgus alpina darwazica; Wyatt & Omoto, 1966: 196 (pro parte; Anjuman Pass).

Pyrgus alpinus pseudoalpinus; De Jong, 1972: 49; 1975a: 7.

External characters (pl. 2 figs. 13, 14). — Length of forewing, ♂ (11.7-) 12.4-14.1 mm; ♀ as large as ♂, but one ♀ from Astana (Panjshir Valley, Afghanistan) measures 15 mm. Upper- and underside exactly like *P. alpinus*

alpinus. There is much variation in the intensity of the white spotting on the upperside of the hindwing. The most strongly spotted specimens are found in Chitral, where some are still more strongly spotted than *P. alpinus alpinus*. As far as can be judged from the available material the variation is not clinal, but more material may indicate a gradually increasing intensity of the spotting from south to north.

Diagnostic notes. — Confusion can arise only with *P. alpinus alpinus*. For a reliable identification genital examination is necessary.

Distribution (fig. 19). — N. Kashmir (Baltistan, Gilgit, Hunza) to Vakhan, and through Chitral to Central Hindu-Kush. The southern-most localities in Kashmir are Astor and Babusar Pass; about 60 km south of Astor, at the Burzil Pass, is the nearest locality of ssp. *cashmirensis*. Sympatric with *P. darwazicus celsimontius* (Koh-i-Munjan, Anjuman Pass).

Material examined. — 62 ♂, 28 ♀, including ♂ paratype of "*Pyrgus cashmirensis pseudoalpinus* Alberti" (Baroghil Pass) (BMNH, CMP, CN, LNK, RMNH, ZMA, ZSM). Localities: Kashmir: Babusar Pass, Chilas, Astor, Batura, Gilgit, Punial, Mushkin, Shandu L., Yasin, Nagar Baltar, Nagar Dabaie, Raminj Nullah, Ultar Nullah. Chitral: Chitral, Madaglasht, Garogar, Bangol Pass, Retreat, Wall. Vakhan: Wazit, Sarhad, Issik V., Istmes V., Kotal-e-Sargaz. Badakhshan: Koh-i-Munjan, Ghawas Valley, Anjuman Pass. Parwan: Astana (Panjshir Valley). In the BMNH there is a male from Safed Koh that geographically belongs to ssp. *pseudoalpinus*, but that is small (length forewing 10.8 mm) and indistinguishable from ssp. *pumilus*. The specimen is, however, not very well prepared and the specimen is considered to belong to ssp. *pseudoalpinus* till more material is available.

***Pyrgus cashmirensis pumilus* subspec. nov.**

Pyrgus darwazicus; Von Rosen, 1921: 99 (pro parte).

External characters (pl. 2 figs. 15, 16). — Small, length of forewing ♂ 10.4-11.9 mm, ♀ 11.5-13.1 mm. Upper- and underside of forewing spotted as in ssp. *cashmirensis*, but median spot 2 about equidistant from median spot 3 and central cell spot. Upperside hindwing intermediate between ssp. *cashmirensis* and ssp. *pseudoalpinus*, i.e. more extensively marked than in ssp. *cashmirensis*, with at least part of the submarginal spots indicated by greyish scales, but spots fainter than in ssp. *pseudoalpinus*, median spot 4-5 narrower and subternal spots not conspicuously white, though in some females the latter spots are rather conspicuous. Ground colour of underside hindwing a dark olive brown as in ssp. *pseudoalpinus*, not cold greenish grey as usually found in ssp. *cashmirensis*.

Diagnostic notes. — On the upperside this subspecies is suggestive of small specimens of *P. darwazicus distinctus*, with which it is partly sympatric. Apart from its smaller size, ssp. *pumilus* can be distinguished by the larger and whiter spots on the underside of the hindwing, especially basal spot 7 that is usually very small in *P. darwazicus distinctus*, and by the warmer tinge of the ground colour. By the same characters ssp. *pumilus* can be distinguished from the equally small *P. darwazicus celsimontius*, which can be rather similar but is not sympatric with it.

Distribution (fig. 19). — N. Badakhshan, W. and NW. Pamir, Hissar Mts. Sympatric with *P. darwazicus darwazicus* (Anzob Pass, Tuptschek, Jaschilkul near Tuptschek) and *P. darwazicus distinctus* (Khwahan, Shiva, Khorog). I also consider a rather large male from Kotal-e-Zardeu (15 km N. of Baharak) (length of forewing 12.5 mm) to belong to this subspecies, as its spotting agrees with that of the more northern populations of ssp. *pumilus* and disagrees with that of the more southern populations of ssp. *pseudoalpinus*. It is possible that this specimen indicates an intermediate population.

Material examined. — Holotype ♂, N. Afghanistan, Badakhshan, Nasher to Kotal-e-Kamkhas, 3000-3500 m, leg. Brade & Naumann (CN). Paratypes: 5 ♂, 2 ♀, Badakhshan, Darrah-e-Kuf, 2480 m, vic. Nasher, 16.7.1972, leg. Brade & Naumann (CN); 7 ♂, 1 ♀, Badakhshan, 5 km NE. Kotal-e-Kamkhas (Khwahan), 3500 m, 16.7.1972, leg. Brade & Naumann (CN); 1 ♀, Badakhshan, Khwahan (Darwaz), Pari Kham, 2500 m, 31.7.1972, leg. Brade & Naumann (CN); 1 ♂, Badakhshan, Shiva Mts., 8500', 19-27.7.1960, leg. Colin Wyatt (LNK); 1 ♂, Tadjikistan, Khorog, 2700 m, 25.7.1965, leg. A. Tsvetajev (RMNH). Further material: 1 ♀, Shiva Mts (LNK); 2 ♂, Tuptschek (ZSM); 1 ♂, Jaschil-kul (near Tuptschek) (ZSM); 1 ♀, Anzob Pass (Hissar Mts.) (RMNH).

PHYLOGENY

There is no sense in speaking about the phylogeny of a group if we are not sure of its monophyly (sensu Hennig, 1966). Here we meet the first problem. The only character state shared by the three species that is apparently apomorphic with regard to the states found in other Palaearctic *Pyrgus* species, is the lack of a costal fold in the male. As stated earlier (De Jong, 1975b), the costal fold is a character that has apparently been lost many times during the evolution of the Pyrginae (even in the genus *Pyrgus* where it is absent in some American species), so that the absence of a costal fold in the species of the *alpinus* group is a poor indication of their common ancestry. There is, however, another, non-morphological character that in this case

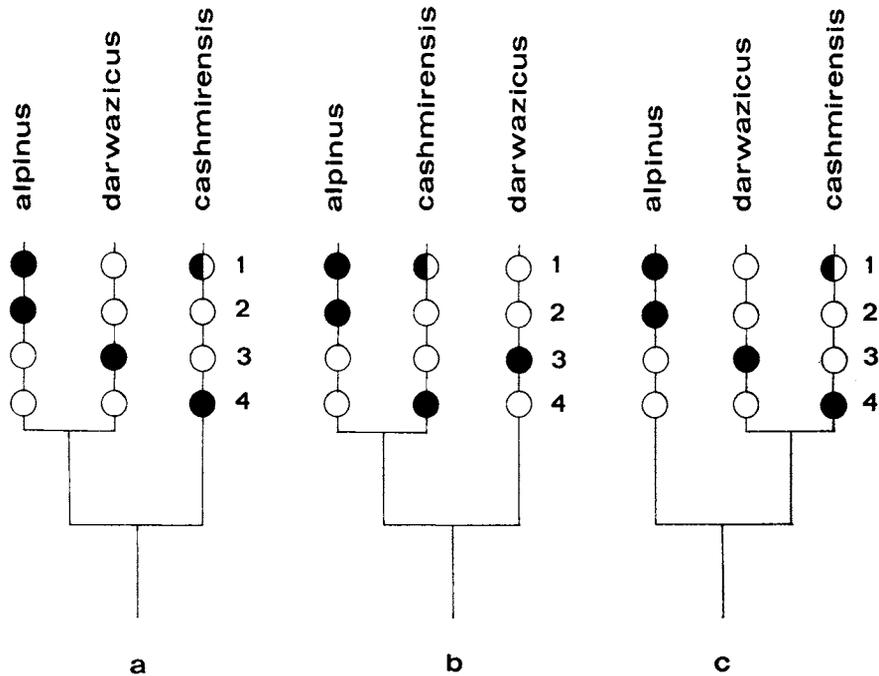


Fig. 20. The three possible phylogenetic trees for the *Pyrgus alpinus* group. The numbers refer to the characters as dealt with in the text. ○ = plesiomorphous state, ● = apomorphic state, ◐ = apomorphic state only in part of the populations.

can play a part in the determination of the monophyly of the group, viz. distribution. The three species are to a certain extent geographically vicarious, and in a very large part of their combined distribution areas they are the sole representatives of the genus. If the loss of the costal fold occurred independently during the evolution of each of the three species, and if each species had a sister species outside the group, the geographical vicariance would be very improbable. Moreover, the *alpinus* group is largely vicarious geographically with the likewise cold-adapted *centaureae* group, which occurs in the European mountains and in the northern parts of the Holarctic Region (De Jong, 1972). Morphologically the groups are fairly close and their vicariance may point to a sister group situation. This is a further argument to consider the *alpinus* group monophyletic.

As the group comprises only three species it does not seem very important to speak about the phylogenetic relationship within the group. The group is, however, illustrative of some problems often met with in phylogenetic research, and for that reason it has at least a heuristic value to deal with the phylogeny here.

For a monophyletic group of three species, three phylogenetic trees are possible, see fig. 20. To select the correct one we must try to indicate synapomorphous character states in two of the three species, showing that the two species form the sister group of the third species, i.e. that they are more closely related to each other than to the third species. It was shown above that the differences between the species are small with respect to the variation within the species, and only four characters are reasonably constant within the species so that they can be used here. Applying the argument of outgroup comparison (cf. De Jong, 1978) the plesiomorphous and apomorphous states of these characters are as follows:

1. Subtornal spots on hindwing upperside:
plesiomorphous — not better developed than other submarginal spots; *P. darwazicus*, *P. cashmirensis* (pro parte); apomorphous — conspicuous, much better developed than other submarginal spots; *P. alpinus*, *P. cashmirensis pseudoalpinus*.
2. Ventral sclerotization of eighth abdominal segment of female:
plesiomorphous — continuous antevaginally; *P. cashmirensis*, *P. darwazicus*; apomorphous — interrupted antevaginally; *P. alpinus*.
3. Shape of cucullus:
plesiomorphous — elongate, proximal edge oblique; *P. alpinus*, *P. cashmirensis*; apomorphous — more rounded, proximal edge less oblique; *P. darwazicus*.
4. Apex of antistylus:
plesiomorphous — rounded or tapering to an obtuse point; *P. alpinus*, *P. darwazicus*; apomorphous — truncate, with a straight edge; *P. cashmirensis*.

It appears that synapomorphy occurs only in character 1. Consequently, the other characters are useless for making a choice between the alternative phylogenetic trees. And even the first character is of little use, as its apomorphous state occurs in *P. cashmirensis* in one subspecies only (ssp. *pseudoalpinus*), and to some extent in the females of another subspecies (ssp. *pumilus*). If this character state arose only once in the evolution of the group, the correct phylogenetic tree would be the one given in fig. 20b. It would not only mean that the species *P. cashmirensis* was a paraphyletic taxon (this could, theoretically, be possible if the evolutionary speed of *P. alpinus* was very much higher than that of its sister group), but also that the other apomorphous character state of *P. cashmirensis* (character 4) arose twice, or arose once and changed back to its original state in *P. alpinus*. This sequence of events is much less probable than the assumption that the

occurrence of obvious subternal spots in *P. alpinus* and part of *P. cashmirensis* is due to parallel evolution.

Consequently there is no argument for making a choice between the alternative phylogenetic trees. It does not influence the classification, the denomination "*alpinus* group" being sufficient to indicate the relationship. Previously (De Jong, 1972) I used the term superspecies for what is now recognized as the *alpinus* group; the large geographic overlap of the species demonstrated in this paper, makes the application of the term superspecies less appropriate.

GEOGRAPHIC VARIATION AND CHARACTER DISPLACEMENT

The characters in which geographic variation occurs, are mainly size and wing markings. It is remarkable that the widest range of variation of the group as a whole occurs in the area where the three species meet or are sympatric. To analyse this problem further, the variations in size and wing markings are treated separately.

1. Size. *P. alpinus* is constant in size throughout its range, except in the area where it is supposed to come into contact with *P. cashmirensis*, where either *P. alpinus* or *P. cashmirensis* is smaller. *P. cashmirensis* is constant in size throughout its range, except in the area where it comes into contact with the larger forms of *P. darwazicus* and *P. alpinus*, where it is smaller. The range of *P. darwazicus* almost entirely coincides with the western part of the range of *P. cashmirensis*; *P. darwazicus* is large where *P. cashmirensis* is small, and vice versa; where *P. darwazicus* and *P. alpinus* probably meet, they are equally sized.

In short, almost everywhere two species meet they differ in size, though elsewhere they may be equally large.

2. Wing markings. The variation in wing markings mainly occurs in *P. cashmirensis* and *P. darwazicus*, which both have dark, intermediate, and well-marked forms. The intermediate forms are rather similar, but the dark form of *P. darwazicus* is darker than that of *P. cashmirensis*, and the well-marked form of *P. cashmirensis* is much more extensively spotted than that of *P. darwazicus*. The variation in extension of wing markings in *P. alpinus* is neglectable. *P. alpinus* and *P. cashmirensis* are almost identical externally where they meet, though the *alpinus*-like form of *P. cashmirensis* is at most partly sympatric with *P. alpinus*. *P. darwazicus* and *P. alpinus* are never close in external characters; where both species probably meet, they are most different from each other. *P. darwazicus* is almost entirely sympatric with the western populations of *P. cashmirensis*. The intermediately spotted *P. cashmirensis* form flies with the darkest as well as with the most extensively

	alpinus ssp.	cashmirensis ssp.	darwazicus ssp.	
size		pumilus ↙	darwazicus ○	sympatry observed
markings		○	↙	
size		pumilus ↙	distinctus ○	
markings		○	○	
size		pseudoalpinus ○	celsimontius ↙	contact supposed
markings		↙	○	
size	alichurensis ↙	pseudoalpinus ○		
markings	○	↙		
size	alpinus ○	pumilus ↙		contact supposed
markings	↙	○		
size	alpinus ○		darwazicus ○	contact supposed
markings	↙		↙	

TABLE I

Character shifts in areas where subspecies of *Pyrgus alpinus*, *P. darwazicus* and *P. cashmirensis* probably or actually meet. Circles indicate that no shift has taken place; arrows indicate convergent (towards the partner) or divergent (away from the partner) shifts.

spotted form of *P. darwazicus*, while the intermediately spotted *P. darwazicus* form flies with the most extensively spotted *P. cashmirensis* form.

In summary, with regard to external characters *P. alpinus* and *P. cashmirensis* are most similar where they meet, *P. alpinus* and *P. darwazicus* are most dissimilar in the area of contact, and *P. cashmirensis* and *P. darwazicus* are rather similar in some, and dissimilar in other areas where they occur together. This pattern of variation is different from, and even partly the reverse of, the pattern found in the variation of size, so that wherever two species meet they differ either in size, or in wing markings, while the forms that are most similar in size as well as in wing markings are allopatric. The situation is summarized in Table 1.

Both patterns of variation seem to show elements of the well-known phenomenon of character displacement, either divergent (variation of size and of wing markings) or convergent (variation of wing markings). In an interesting treatment of the phenomenon, Grant (1972) defined character displacement as follows: "Character displacement is the process by which a morphological character state of a species changes under natural selection arising from the presence, in the same environment, of one or more species similar to it ecologically and/or reproductively".

To find out how much of the variation can actually be contributed to character displacement the following questions have to be answered: a. what is the direction of the shift in contact areas; b. is there a competitive advantage in the differences or similarities found in the sympatric populations; and c. did the character shift take place when the populations concerned were in contact or did it originate in allopatry?

The first question is an evolutionary one, as it bears upon the discrimination between plesiomorphous and apomorphous character states. As regards the size, the length of the forewing of the large forms in the *alpinus* group (about 11.5-14 mm) corresponds with or rather is slightly less than the average length of the forewing of the other Palearctic *Pyrgus* species. It is therefore plausible to suppose that the small size of some forms of the *alpinus* group is a derived state. For the same reason it is plausible to suppose that the intermediately spotted forms are closest to the most recent ancestor of the *alpinus* group; forms as dark as the nominate subspecies of *P. darwazicus* are generally restricted to the subspecific variation in other *Pyrgus* species, while the conspicuous subternal spots on the upperside of the hindwing in *P. alpinus* and part of *P. cashmirensis* are not found at all in other *Pyrgus* species (see also under phylogeny).

The second question is an ecological one. By lack of ecological data it is difficult to evaluate the possible competitive advantage of the character shifts.

Although there must be a positive correlation between food intake by the larvae and size of the full-grown insect, the differences in size can help to minimize competition for food only if the species feed upon the same plant species. At the moment the food plants of the *alpinus* group are unknown. Still more uncertain is the advantage of having different or similar wing markings. If wing markings are similar and if the similarity is not based on symplesiomorphy, we may think of mimicry. In the present study it could apply only to the similarity between *P. alpinus* and *P. cashmirensis pseudoalpinus*. In this case mimicry would be a good explanation of the parallel evolution of the subternal spots on the hindwing in both lines, but as long as no predator and no advantage of being similar is known, it seems more realistic to attribute the similarity to the phenomenon known as Vavilov's Law of parallel series of variation. (Although in my opinion the study of mimicry has revealed some convincing cases of convergent character displacement, the phenomenon of mimicry was not mentioned at all by Grant, 1972.)

The third question is mainly a historical-geographical problem. Even if the character shifts found in the *alpinus* group minimize competition, we can only speak of character displacement if the two species of which at least one shows a character shift, were in contact with each other when the shifting took place, as only in that case the shift can be supposed to be the result of the presence of the other species. In other words, a choice must be made between two alternatives: a. two species can live together because they are different or similar (allopatric origin of shift); and b. two species are different or similar because they live together (sympatric origin of shift). In general it is impossible to decide between the alternatives, apart from the following reasoning which is restricted to the change in size, as the possible competitive value of this change is conceivable.

If two or more species are as closely related phylogenetically as apparently the species of the *alpinus* group are, it is highly improbable that the size of the insects is affected by the same selective force in divergent ways. So if the size has indeed been affected in different ways, it must be the result of different selective forces. It means that the shift either originated in allopatry or, if in sympatry, it was the result of a selective force working on only one of the species. In the latter case, the most obvious possible selective force working on only one of two sympatric species is the presence of the other species. If the shift in size originated in allopatry, and thus is not the result of competition between the taxa in question, there is no reason for subsequent complete sympatry, as it was not the similarity in size that acted as a barrier against sympatry and it is not the difference in size that makes the sympatry

possible. In the alternative case, however, sympatry is facilitated by the difference and eventually more or less complete sympatry is to be expected.

Turning to the *alpinus* group, there are two pairs of sympatric taxa in which a difference in size may reduce competition, viz. *P. darwazicus darwazicus* + *distinctus* / *P. cashmirensis pumilus* and *P. cashmirensis pseudo-*

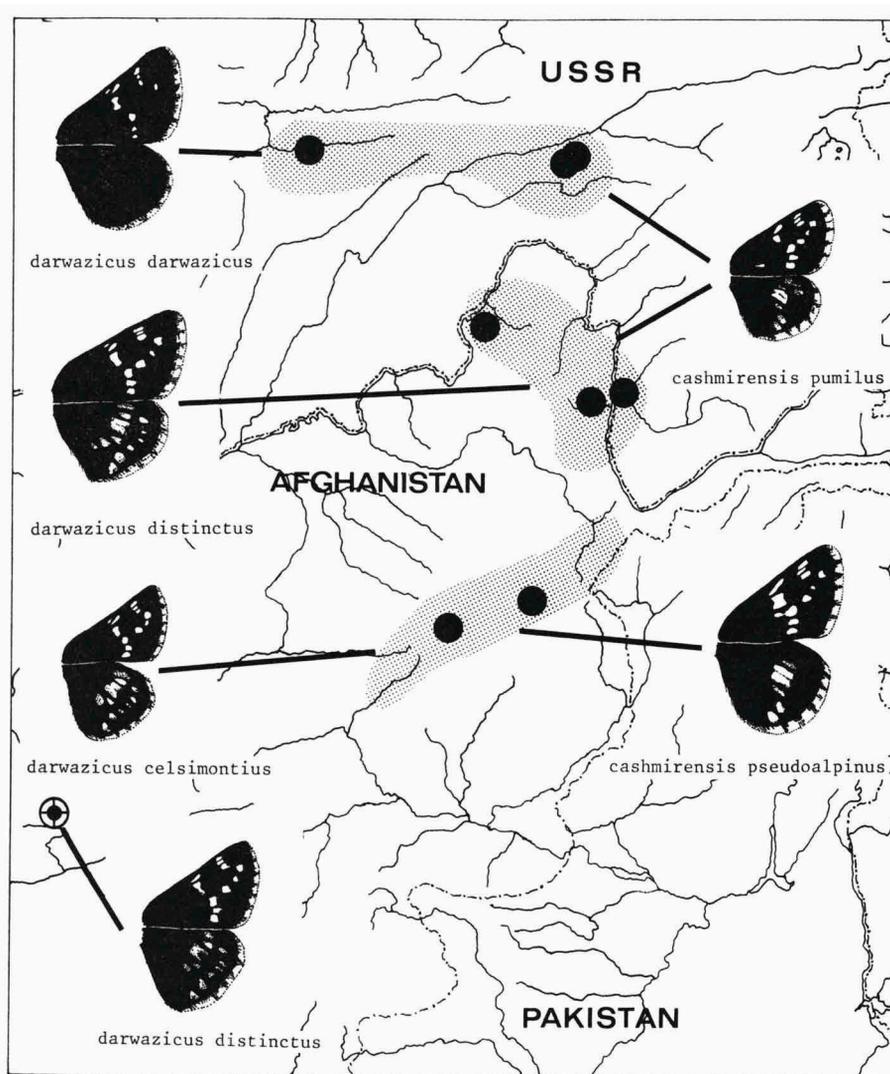


Fig. 21. Geographic variation of *Pyrgus darwazicus* and *P. cashmirensis* in areas of sympatry. Where *P. darwazicus* is large, *P. cashmirensis* is small, and vice versa. The wings have been drawn at the same scale. Black dots indicate localities where both species have been found flying together; the supposed areas of sympatry are grey.

alpinus / *P. darwazicus celsimontius* (in the other pairs listed in table 1 the sympatry is deduced from the distribution, but has not yet actually been observed). In the first pair sympatry is more or less complete, i.e. neither taxon is known to occur outside the common area. Outside this area of sympatry *P. cashmirensis* is obviously larger, and *P. darwazicus* smaller. Starting from the assumption that the small size of *P. cashmirensis pumilus* is a derived state (see above), it is plausible to suppose that the small size is an adaptation to living in an area where already a phylogenetically and ecologically closely related species is present. If not so, why is *P. cashmirensis* small only where it meets large relatives and why does not the neighbouring large *P. cashmirensis pseudoalpinus* occur together with the equally large *P. darwazicus* forms?

In the other pair, sympatry is incomplete; although *P. darwazicus celsimontius* probably does not occur outside the area of *P. cashmirensis pseudoalpinus*, the latter has a much more extensive area. It is meaningful that it is the large sized taxon that has the wider distribution area. The most plausible inference is that the small size of *P. darwazicus celsimontius* is the result of selection pressure caused by the presence of the larger *P. cashmirensis pseudoalpinus*, and not the reverse. If this inference is correct, the need of being small is absent outside the area of the larger taxon. It may therefore be significant that a specimen of *P. darwazicus*, indistinguishable from the large ssp. *distinctus*, was found at Panjao, south of the area of ssp. *celsimontius*, while ssp. *distinctus* is distributed north of ssp. *celsimontius*. As far as known Panjao lies far outside the area of *P. cashmirensis pseudoalpinus* and this may be the reason why at Panjao a large form can exist. This observation is, however, based on a single specimen only.

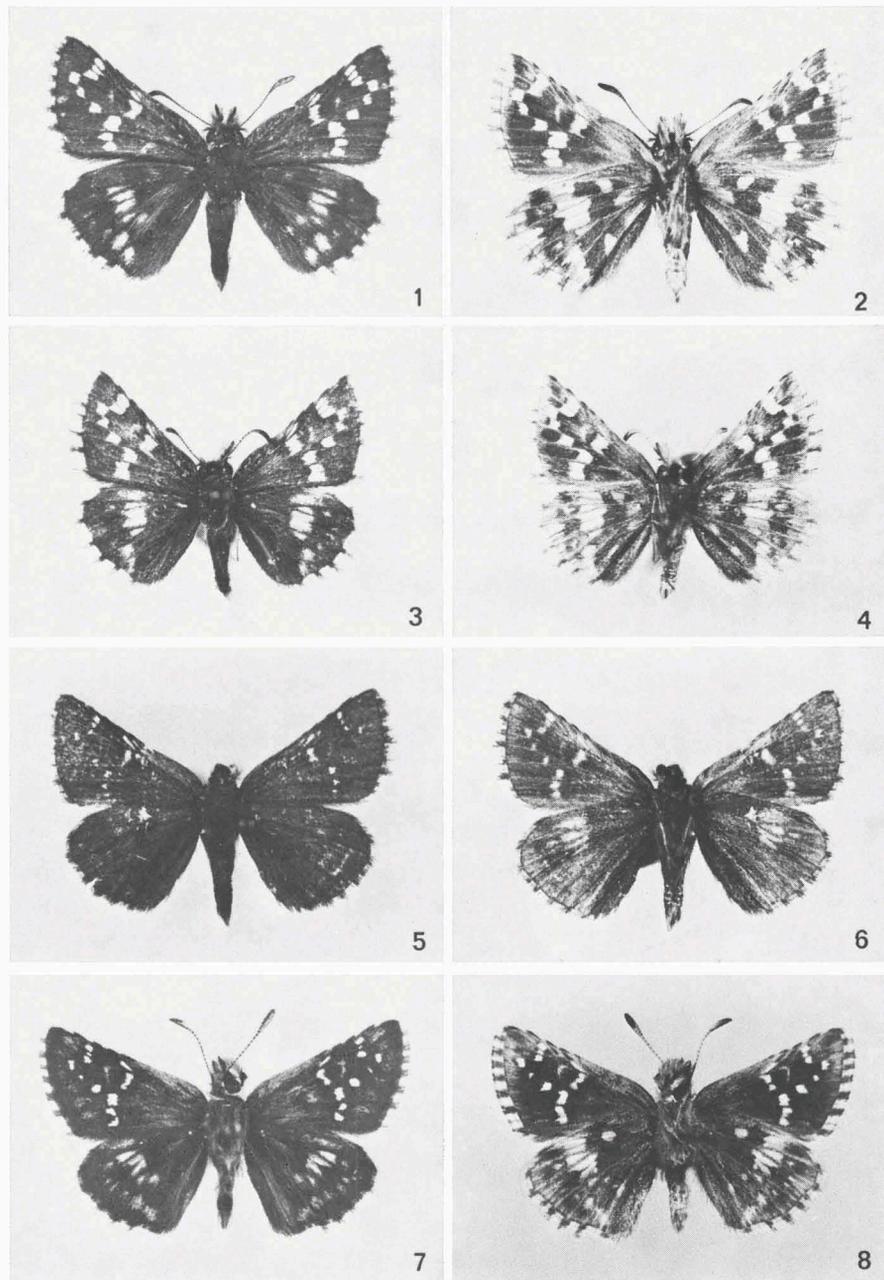
Summarizing, character displacement offers a plausible explanation for differences in size found between some sympatric populations of the *P. alpinus* group. The situation has been illustrated in fig. 21. For other cases of sympatric populations differing in size or in wing markings, no satisfactory explanation can be given at the moment due to lack of information.

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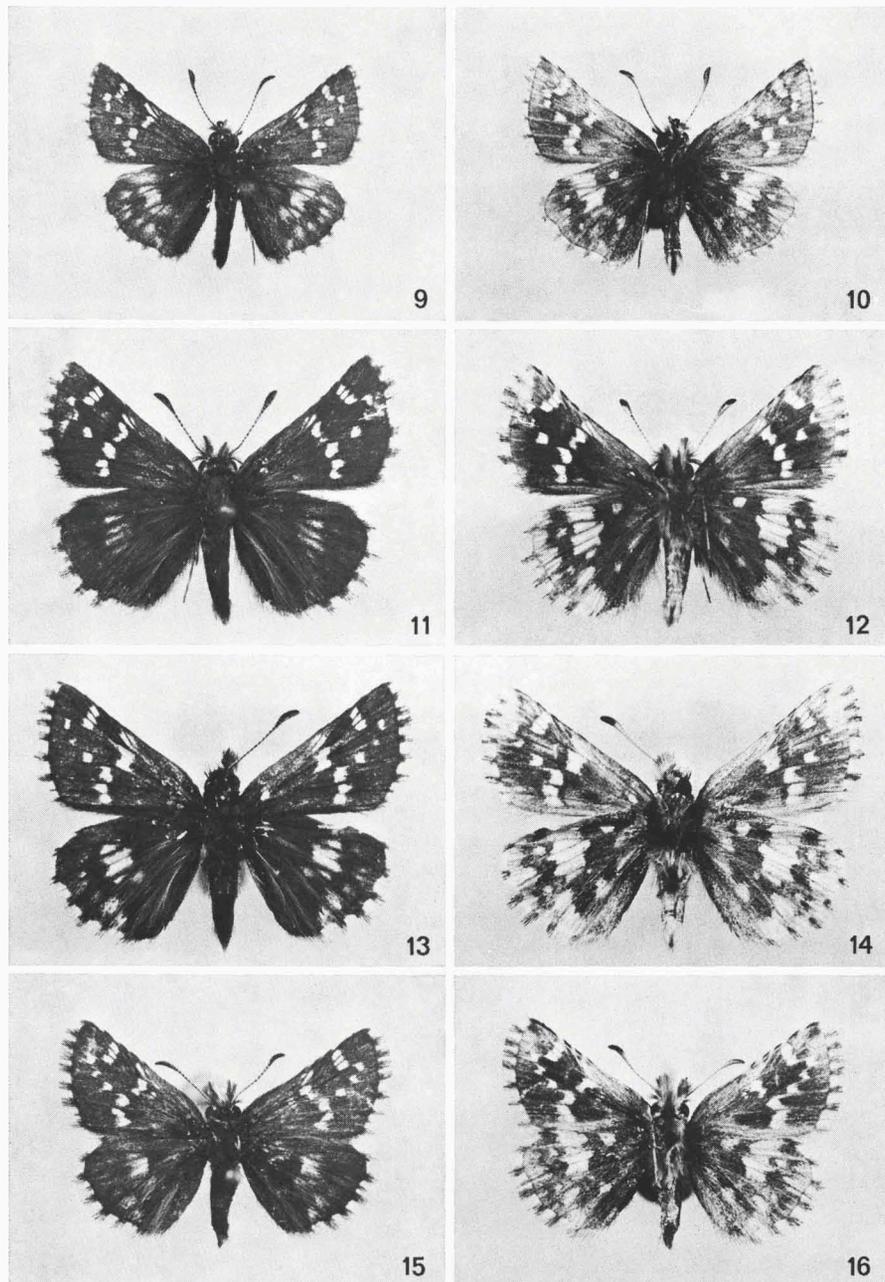
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Figs. 1-8. Upper (left) and undersides (right) of males of *Pyrgus* species. 1-2, *P. alpinus alpinus*, Ispajran, N. Alai (RMNH); 3-4, *P. alpinus alichurensis*, holotype, S. Alichur Mts., Koytezek Pass (RMNH); 5-6, *P. darwazicus darwazicus*, Hissar Mts., Anzob Pass (RMNH); 7-8, *P. darwazicus distinctus*, paratype, Badakhshan, Kotal-e-Zardeu (LNK).
All photographs 1.8 X natural size.



Figs. 9-16. Upper (left) and undersides (right) of males of *Pyrgus* species. 9-10, *P. darwazicus celsimontius*, Badakhshan, Bala Quran (ZSM); 11-12, *P. cashmirensis cashmirensis*, Himachal Pradesh, Chandra River (CS); 13-14, *P. cashmirensis pseudoalpinus*, Chitral (RMNH); 15-16, *P. cashmirensis pumilus*, holotype, Badakhshan, Nasher to Kotal-e-Kamkhas (CN). All photographs, 1.8 × natural size.