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Sphaleroptera alpicolana (FRÖLICH 1830) (Lepidoptera: *Tortricidae*, *Cnephasiini*): a species complex

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Sphaleroptera alpicolana **(FRÖLICH 1830) (Lepidoptera: *Tortricidae*, *Cnephasiini*): Ein Spezies Komplex**

Summary

Sphaleroptera alpicolana (FRÖLICH 1830) is a locally common day-flying high Alpine species previously considered to occur in the German, Austrian, Swiss, Italian and French Alps, and the Pyrenees. The females have reduced wings and cannot fly. However, a study of material from the known range of the species has shown that "*Sphaleroptera alpicolana*" is really a complex of several taxa. *S. alpicolana* s.str. occurs in the central part of the Alps, in Switzerland, Italy, Austria and Germany. A new subspecies, *S. a. buseri* ssp.n. is described from the Valais (Switzerland). Four new species are described, based on distinct differences in the male and female genitalia: *S. occidentana* sp.n., *S. adamelloi* sp.n., *S. dentana* sp.n. and *S. orientana* sp.n., with the subspecies *S. o. suborientana*. Distribution maps are given for all taxa and where known, the early stages and life histories are described. The role of the Pleistocene glaciations in the speciation process is discussed.

Zusammenfassung

Sphaleroptera alpicolana (FRÖLICH 1830) ist eine lokal häufige, Tag fliegende, hochalpine Art, bisher aus den deutschen, österreichischen, schweizerischen, italienischen und französischen Alpen, und den Pyrenäen bekannt. Die Weibchen haben reduzierte Flügel und können nicht fliegen. Eine Studie von Exemplaren aus dem gesamten bekannten Verbreitungsgebiet der Art hat jedoch ergeben, dass „*Sphaleroptera alpicolana*" tatsächlich einen Komplex aus mehreren Taxa darstellt. *S. alpicolana* s.str. kommt in den Zentralen Alpen, in der Schweiz, in Italien, Österreich und Deutschland vor. Eine neue Subspezies, *S. a. buseri* ssp.n. wird aus dem Wallis (Schweiz) beschrieben. Vier neue Arten werden beschrieben, basierend auf klaren Unterschieden in den männlichen und weiblichen Genitalien: *S. occidentana* sp.n. (Frankreich, Italien, Schweiz), *S. adamelloi* sp.n. (Italien), *S. dentana* sp.n. (Österreich, Italien) und *S. orientana* sp.n. (Österreich, Italien) mit der Subspezies *S. o. suborientana* (Italien). Verbreitungskarten werden für alle Taxa gegeben und, wo bekannt, werden die erste Stadien und Biologien beschrieben. Die Rolle der pleistozänen Vergletscherungen im Speziesbildungs-Prozess wird diskutiert.

Keywords: Lepidoptera, *Tortricidae*, new species, Ice-Ages, Quarternary, speciation, nunatak

Introduction

Tortrix alpicolana was described in 1830 by Dr v. Frölich in Geyer's supplement to Jakob Hübner's 'Sammlung europäische Schmetterlinge'. Frölich's specimens came from the Alps of 'Algau' (Allgäu) in southern Germany. In the original description, no mention is made of the fact that the female has reduced wings and cannot fly. Indeed, the female figured in that work has normal wings and must therefore be a male.

GUENÉE (1845) included *alpicolana* in a new genus *Sphaleroptera*, without fixing it as the type species. FERNALD (1908) erected the new genus *Euledereria* for *alpicolana* because he considered that when STEPHENS (1852) had first restricted the use of this genus to the species *ictericana* HAWORTH 1811 (now a junior synonym of *longana* HAWORTH 1811), he had effectively fixed the type and caused it to be placed in synonymy with *Cnephasia* CURTIS, 1826. However, simply restricting the use of a genus to a single species is not sufficient to fix a type species of a genus according to the current Code of Zoological Nomenclature (International Commission on Zoological Nomenclature, 1999). DESMAREST (1857) was the first to correctly fix the type species of *Sphaleroptera* (incorrectly written as '*Phaleboptera* Gn.') according to the current Code and he assigned '*alpicolana* Hübner' as the type (LERAUT 1978).

Sphaleroptera continued to be used in the European literature, but *Euledereria* has been used in several more recent publications, following OBRAZTSOV (1955).

Sphaleroptera alpicolana is generally regarded as a locally common day-flying species of the higher Alpine regions, occurring from the Austrian Alps of Styria and Carinthia westwards to the French Alps and the Pyrenees. The female is brachypterous. The species occurs on rock-strewn Alpine meadows and screes above the timber line (Fig. 1B,C,E,F), typically where cushion plants such as *Silene aucaulis* (Moss Campion, Caryophyllaceae) (Fig. 1B) and *Saxifraga oppositifolia* (Purple Saxifrage, Saxifragaceae) (Fig. 1A) grow. The males are very variable and several individual forms have been described. However, a study of the genitalia shows that '*Sphaleroptera alpicolana*' is really a complex of several taxa and these are described here.

Systematic list of species

Sphaleroptera alpicolana (FRÖLICH 1830)
Sphaleroptera alpicolana buseri ssp.n.
Sphaleroptera occidentana sp.n.
Sphaleroptera adamelloi sp.n.
Sphaleroptera orientana sp.n.
Sphaleroptera orientana suborientana ssp.n.
Sphaleroptera dentana sp.n.

Methods and materials

Sphaleroptera material is generally fairly scarce among collections, especially females. Furthermore, with time, museum specimens lose their natural colours and turn brownish. Although a lot of interesting material was available from various museums and private collections, the study was heavily dependent on the collection of fresh material, which has been undertaken over the last twenty years. I have been helped in this by several entomologists, who are acknowledged below, but I am particularly indebted to Peter Huemer of the Tiroler Landesmuseum, Innsbruck, for providing much interesting material from Austria, Italy and France.

Males fly only during sunshine and then usually in the morning, especially in the couple of hours after sunrise. They like to alight on sun-drenched rocks, restlessly running around before flying off again in a rapid erratic flight, often returning again to the same spot (Fig. 2A). Females cannot fly, but if disturbed they can very actively hop like a small grasshopper to escape predators and rapidly scurry away among the rocks and vegetation (Fig. 2B). They can be found by turning over rocks and looking under potential foodplants, but the use of a beesmoker can be more successful (WEBER 1945). Another particularly successful method has been to sink a ground trap in a likely area and leave it for several days. In this way 23 females and 11 males (presumably attracted by the females) were collected in one Austrian locality. This method is good for faunistic studies, although regular visits should be made to prevent too many specimens being killed. Some females could be obtained by breeding from larvae, but most often the larvae have finished feeding before the breeding areas can be easily reached. Unlike with the genus *Sattleria* (Gelechiidae) (HUEMER and SATTLER 1992), young larvae have not been found during the flight period, so there is no evidence for a biennial development. Pupae have been found under rocks and spun up among the foodplant. Thomann found females towards evening sitting on flowering *Aster alpinus* (Alpine Aster, Compositae) in Parpan, Switzerland, but it is not clear whether they were actually feeding on the flowers (MÜLLER-RUTZ 1922). This would be an important observation, as non-feeding is considered to be a precondition for flightlessness (SATTLER 1991).

All male specimens were either dissected and the genitalia prepared on microscope slides (ROBINSON 1976) or they were identified by their genitalia without dissection. The tip of the phallus (nomenclature following KRISTENSEN 2003) can usually be seen sufficiently for identification by removing some of the anal hairs, but care should be taken not to break the tip of the phallus. The male genitalia, in particular the valvae, are difficult to prepare on a microscope slide in a uniform manner. For this reason, the left-

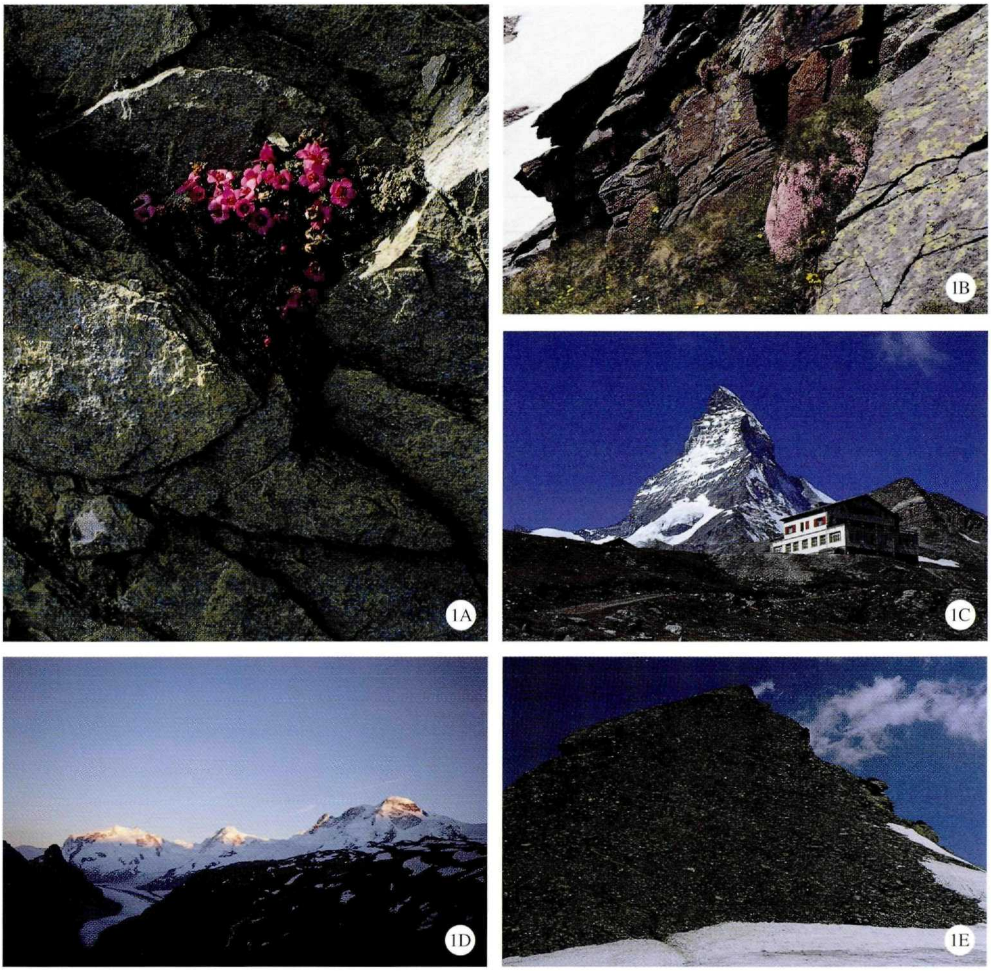


Fig. 1: **A** – *Saxifraga oppositifolia*, Switzerland: Mettelhorn, VS, 3400m, from which *Sphaleroptera a. buseri* was bred; **B** – Typical habitat of *Sphaleroptera* spp., showing large cushion of *Silene acaulis*, Switzerland: Moiry, VS, 3000m; **C** – Schwarzsee, Zermatt, VS, 2500m, habitat of *S. occidentana*; **D** – The Gorner Glacier, which splits populations of *S. a. buseri* on left and *S. occidentana* on right (left foreground: Riffelhorn, 2928m; left of centre: Monte Rosa, 4633m, centre: Liskamm, 4527m; right: Breithorn, 4160m; extreme right foreground: Trockenersteg, 2639m); **E** – Switzerland, Mettelhorn, VS, peak (3406m) rises above permanent snow field, habitat of *S. a. buseri*; **F** – Switzerland: Nufenen Pass, TI, 2620m, habitat of *S. a. alpicolana*.

hand valve (viewed ventrally) was usually removed and placed under a separate cover slip, together with the phallus, with a relatively small amount of Euparal, allowing a certain amount of flattening of the valva. The remaining genitalia parts were mounted with the valva not opened and in a sufficient amount of Euparal to prevent distortion. Where the phallus length is given (*S. orientana*), this was measured along

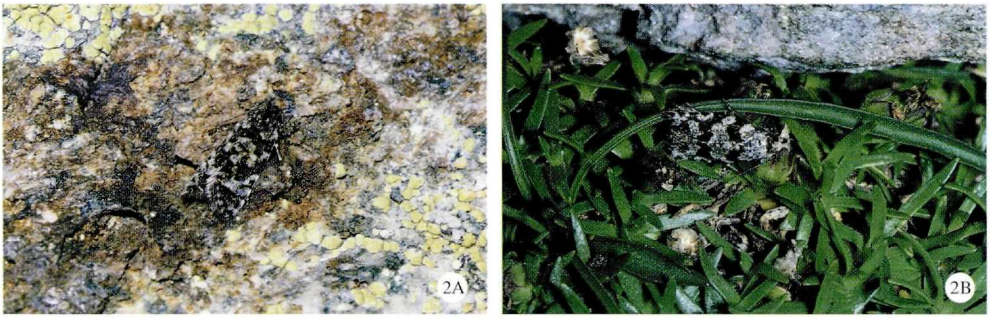


Fig. 2: A – Male of *Sphaleroptera occidentana* (Schweiz, Zermatt, Schwarzsee, 23.7.1984, Holotype); **B** – Female of *S. a. buseri* (Schweiz, Zermatt, Mettelhorn e.l. *Saxifraga oppositifolia*, 17.8.1984, paratype).

a straight line from the top of the opening in the shaft where the ejaculatory duct enters, to the tip, inclusive of any sclerotized projection. Measurements were made to the nearest 0.025 mm using a scale with 0.05 mm gradations. The female genitalia were usually prepared by separating the abdomen between the 6th and 7th segments and the tergite of the 7th segment was detached at one side and folded out to the left, thereby clarifying the background to the antrum and sternite. Sometimes the sternite was also separated from the antrum.
The distribution maps were prepared using the software program DMAP (MORTON 2001). The grid used is 8' longitude and 5' latitude (approximately 10 km x 10 km).

Material was received from the following collections:
BMNH – The Natural History Museum, London, UK
ETHZ – Eidgenössische Technische Hochschule, Zürich, Switzerland
KML – Kantonal Museum Liestal, Switzerland
MCSN – Museo Civico di Storia Naturale, Verona, Italy
MHNG – Muséum d'histoire naturelle, Geneva, Switzerland
MNHP – Muséum national d'histoire naturelle, Paris, France
MTMB – Magyar Természettudományi Múzeum, Budapest
NHMB – Naturhistorisches Museum, Basel, Switzerland
NHMBe – Naturhistorisches Museum, Berne, Switzerland
NHMW – Naturhistorisches Museum, Vienna, Austria
TLMF – Tiroler Landesmuseum Ferdinandeum, Innsbruck, Austria
USMC – Università degli Studi di Milano, Italy
ZMHB – Zoologisches Museum der Humboldt Universität, Berlin, Germany (coll. Staudinger)
ZMUC – Zoologisk Museum, University of Copenhagen, Denmark

Plus the private collections of H. Buser†, Sissach, Switzerland, W. Keller, Zizers, Switzerland, J. Klimesch†, Linz, Austria, P. Réal, Lyon, France, Axel Scholz†, Neu-Ulm, Germany and P. Sonderegger, Brügg, Switzerland.

***Sphaleroptera* GUENÉE 1845: 167**
Sphaleroptera DESMAREST 1857: 224
Eulederia FERNALD 1908: 31
Euledereria FERNALD 1908: 59 nom.emend.

***Sphaleroptera alpicolana* (FRÖLICH 1830)**
Sphaleroptera alpicolana f. *obscurana* BURMANN 1958: 4.

Sphaleroptera alpicolana f. *pallidana* BURMANN 1958: 4.
Euledereria alpicolana FRÖLICH 1830. RAZOWSKI 1959 Figs 120, 121, 247, 316.
Euledereria alpicolana FRÖLICH 1830. HANNEMANN 1961 ♂ genitalia Fig. 76.
Euledereria alpicolana FRÖLICH 1830. RAZOWSKI 2002: 76.

Material examined: 98♂, 12♀

Switzerland: 5♂, 11.7.[18]62, [?Jungfrau-]Joch, Jäggi Sammlung [NHMBe] ; 10♂, [Berner Oberland], leg. Rothenbach [NHMBe]; 1♂, Mattmark, 24.VII.1923, Coll. Dr. G. Audéoud [MHNG] GP E.612; 1♂, Saas, Switzerland 7500', 13/8/00, Meyrick Coll., BM 1938–290, [BMNH] BM GP. 23386; 1♂, TI Schweiz, Nufenen Pass, 2620m, 673.2/148.4, 12.8.1984, S.E.Whitebread, [Coll. Whitebread, KML] GP 454; 1♂, VS Schweiz, Sirwoltesee, 2230m, 643.4/118.275, 12.8.1984, S.E.Whitebread [Coll. Whitebread, KML] GP 453; 1♂, Geisspfadsee, s/Binn VS, 2400m 26.6.76, leg. E. de Bros [Coll. Whitebread, KML] GP E.414; 1♂, GR Schweiz, Soglio – Duan, 2600m, 763.1/137.45, 27.8.1981, S.E.Whitebread, [Coll. Whitebread, KML] GP 405; 3♂, GR Schweiz, Bivio, Forcellina, 2550m, 767.6/143.3, 24.7.1990, S.E.Whitebread, ex pupae under rocks [Coll. Whitebread, KML]; 1♂, GR Schweiz, Bivio, Septimer, 1970m, 770.4/146.1, 23.7.1990, S.E.Whitebread [Coll. Whitebread, KML]; 2♂, GR Schweiz, Bivio, Septimer, 2400m, 768.3/143.25, 24.7.1990, S.E.Whitebread [Coll. Whitebread, KML] ; 1♀, Schweiz, GR, Bivio, Forcellina, 2550m, 767.6/143.3, 24.7.1990, leg. S.E.Whitebread, [Coll. Whitebread, KML]; 1♂, Schweiz, GR, Silvaplana, Valetta da Güglia, 776 725 / 150 225, 2200m 28.7.05, leg. Sibylle Stänz [Coll. Keller]; 6♂, S-charl GR, Lajet da Lischana, 823/181, P. 2901 m, 31.7.2002, leg. Sonderegger [Coll. P. Sonderegger]; 1♂,1♀, Schweiz, GR, Bever, Valletta da Bever, 2320m 784.25/157.65, Pupa 10.07.2000, S. Whitebread, Puppe in Gespinst in Silene acaulis Polster e.p. 14.7.2000 [Coll. Whitebread, KML]; 1♂, Albula, Ag/95, 2293 [ETHZ]; 1♂, Davos, D'thäli 8/94, 2293 [ETHZ]; 1♂, D'fth'li 7.8.[18]94 [Coll. Paravicini, NHMB] GP E.442; 6♂, GR Schweiz, Siat, 2300m, 729.95/187.8, 1.8.1988, S.E.Whitebread [Coll. Whitebread, KML]; 1♂, alpicol. Lenzerheide m 2.viii. [Coll. J. Müller-Rutz, NHMB] GP E.434; 1♂, Parpaner Rothorn 2850m 25.viii.16 Dü [NHMBe]; 1♂, alpicol. Ebenalp m vii.89 [Coll. J. Müller-Rutz, NHMB] GP E.430; 1♂, alpicol. Sardonna m 3.viii.04 [Coll. J. Müller-Rutz, NHMB] GP E.431; 1♂, alpicol. Sardonna m 3.viii.04 [Coll. J. Müller-Rutz, NHMB] GP E.432; 1♂, alpicol. Sardonna m 3.viii.04 [Coll. J. Müller-Rutz, NHMB] GP E.435; 1♀, alpicol., Sardonna, f 30.VII.18, leg. J. Müller-Rutz [NHMB] GP E.438; 1♂, alpicol. Urdenfürkli m 10.viii.19 [Coll. J. Müller-Rutz, NHMB]; 1♂, alpicol. Urdenfürkli m 5.viii.21 [Coll. J. Müller-Rutz, NHMB]; 1♂, alpicol., Messmer, m 2.VIII.91 [Coll. J. Müller-Rutz, NHMB] GP E.429; 1♂, alpicolana Alp Hädern m 14.vii.1918 Ad. [Coll. J. Müller-Rutz, NHMB]; 1♂, alpicolana, Alp Grüm, m 4.VIII.23, leg. J. Müller-Rutz [MHNG]; 1♀, Murgsee, Furkel, SG, Juli 1918, leg. P. Weber [NHMBe] – **Italy:** 1♂, 42 / Sph. alpicolana, Stelvio Est. 74 [USMC]; 1♂, Alto Adige Val Venosta, Seebodenspitze m.2700, L. Rocca legit. Ag.930 [MCSN]; 1♂, Campiglio, vii.95 [BMNH]; 1♂, Crodo, 9.viii.95, S.N.A.Jacobs, Coll. BM 1972-522, [Coll. Jacobs, BMNH]; 1♂, Italia sept., Teriolis merid., Laatsch, 1000m, 15.9.1980, leg. Burmann [TLMF]; 1♂, Stilfser Joch, Ende Juli 1895, Rebel [NHMW]; 2♂, Südtirol, Stilfser Joch, 2400m 12.8.67, H. Jüngling leg. [TLMF]; 1♂, Trafoi, [coll. Staudinger, ZMHB]; 1♂, Süd-Alpen, Ortler Gruppe, Umg. Sulden, Kanzel, 2300m, 14.8.69, M. Sommerer leg. [TLMF]; 3♂, Süd-Alpen, Ortler Gruppe, Umg. Sulden, Schaubach Hütte, 2400m, 13.8.69, M. Sommerer leg. [TLMF]; 1♂, Italien, Südtirol-Dolomiten, Pordoipass, 2300m, 25.07.93, A. Scholz [Coll. Whitebread, KML] – **Austria:** 4♂, Austria, Vorarlberg, Brandner Tal 2750m, Wildberg, 22.8.1984, leg. Huemer [TLMF] ; 1♂, Tirol, Samoar Hütte 2600m 5.8.1948, Kappeller, Innsbruck [Coll. R. Kappeller, MHNG]; 2♂, Tirol, Samoar Hütte 2700m 4.8.1948, Kappeller, Innsbruck [Coll. R. Kappeller, MHNG]; 1♀, Tirol, Samoar Hütte ca. 3000m 23.7.1950, Kappeller, Innsbruck [Coll. R. Kappeller, MHNG] GP E.610; 1♂, Tirol, Ötztal Kreuzspitze 3000m 6.8.1948, Kappeller, Innsbruck [Coll. R. Kappeller, MHNG]; 1♂, Teriolis Vent., 2700m 24.7.1938, J.Klimesch, [coll. Jacobs, BMNH]; 1♂, Pitztal, Tirol [?]Kariny [NHMW]; 2♂, 26.7.38, Tirolia, Ötztaler Alpen, Lamvarhütte, leg. R.Lunak [NHMW]; 3♂, Österreich, Ötztaler Alpen, Rettenbachferner 2700m 9.08.92 A. Scholz [Coll. Whitebread, KML]; 1♀, Tirol, Rettenbachtal 2500m 31.7.1950, Kappeller, Innsbruck [Coll. R. Kappeller, MHNG]; 1♂, Nord Tirol, Stubaital Schrankogl 3400m 15.9.1970 Burmann [Coll. R. Kappeller, MHNG] GP E.608; 2♂, Nord Tirol, Stubaital

Schrankogl 3400m 15.9.1970 Burmann [Coll. R. Kappeller, MHNG]; 1♀, Tirol, Alpeiner Moräne 2500m 2.8.1949, Kappeller, Innsbruck [Coll. R. Kappeller, MHNG]; 1♂, Tirol, Stubai Sommerwand 2600m 30.7.1949 Kappeller, Innsbruck [Coll. R. Kappeller, MHNG]; 1♂, Tirol, Fr. Senn Hütte 2600m 28.7.1949, Kappeller, Innsbruck [Coll. R. Kappeller, MHNG]; 1♀, Tirol, Fr. Senn Hütte 2600m 26.7.1949, Kappeller, Innsbruck [Coll. R. Kappeller, MHNG]; 1♂, Zerny leg, Nord-Tirol, Lambsen b. Praxmar, 13.8.28 [NHMW] Razowski GP10850 m [1969], Euledereria alpicolana Fröl.[Mus.Vind. 2728]; 1♂, 1♀, Zerny leg, Nord-Tirol, Acherkogel, 7.8.28 [NHMW] Razowski [♀] GP10851 m [1969], Euledereria alpicolana Fröl.[Mus.Vind. 2729]; 1♀, Nord Tirol, Mandlspitze 2300m 10.8.1971, Kappeller, Innsbruck [Coll. R. Kappeller, MHNG]; 1♂, N. Tirol, Seegrube 2000m 28.8.1968, Kappeller, Innsbruck [Coll. R. Kappeller, MHNG]; 2♂, Nord Tirol, Langer Sattel 2200m 31.7.1970 Kappeller, Innsbruck [Coll. R. Kappeller, MHNG]; 1♀, Tirol, Sattelspitzen 2200m 15.7.1947, Kappeller, Innsbruck [Coll. R. Kappeller, MHNG]; 1♂, Nord Tirol, Gleirsch Joch 2200m 26.7.1971 Kappeller [Coll. R. Kappeller, MHNG]; 1♀, Nord Tirol, Gleirsch Spitze 2300m 1.8.1971, Kappeller, Innsbruck [Coll. R. Kappeller, MHNG] – **Germany:** 2♂, Südbayern, Karwendel M.7.77 1900m, Fr.Zürnbauer, Mü. [TLMF] – **Location not found:** 1♂, Ponte 79. M. [coll. Staudinger, ZMHB]; 1♂, Schneeb [see note below] [USMC] GP E.607.

Description:

Wingspan: males 15.0–20.5 mm, median 18.0 mm, n=80; females 13.0-16.5 mm, median 15.3 mm, n=10

Male (Fig. 3A,B): Head, thorax, palpi, abdomen and legs dark grey, sometimes sprinkled whitish, antennae grey, ringed white. Forewing: Ground colour very variable, from pure white to bluish and shining dark slaty grey; three dark grey or brown angular fasciae at one third (subbasal), often not reaching dorsum, at one half (medial) and at two thirds (subterminal), the latter usually incomplete and not reaching costa; several dark grey or black spots forming a complex, but relatively constant pattern across wing, often joined together to form dark cross-lines; ten such spots present along or just behind costa, the 2nd and 3rd, 5th and 6th and 9th mark the edges of the fasciae, often a straightish line stretching from 7th or 8th costal spot to tornus, several spots also present along, and marking edges of fasciae and about eight along dorsum; all these spots often persisting even in very pale specimens; spots and lines often thinly overlaid with orange scales; ground colour usually forming 5 paler spots between darker costal spots; fringes pale grey; underside pale grey or brown, whitish at base, 9 to 11 whitish costal spots, darker between, sometimes about 6 weaker pale spots along termen, extending into fringe. Hindwing: Uniform brownish grey, fringe pale grey, darker at base forming post terminal line; underside pale brownish grey mixed white, especially along costa, at apex and termen, forming approx. 9 spots.

Female (Fig. 4A-D): Head, thorax, palpi, hindlegs and abdomen white, usually only weakly mixed with darker scales, abdominal tuft usually orange, antennae dark grey, ringed white, hindleg tarsi ringed black, middle and forelegs more extensively marked black. Forewing: Ellipsoid, approx. 0.8x length of male, general pattern similar to male, but ground colour generally much whiter, mixed with few darker scales, and more strongly contrasting with the dark grey to black subbasal and medial fasciae; black spotting typical of the male much less prominent, except four costal spots beyond the medial fascia, but orange scaling equally present. Fringes whitish, often mixed black or brown, sometimes chequered. Hindwing: Very narrow, short and straight; pale brownish grey.

♂ **genitalia** (Fig. 5A-C; Fig. 6A,B; Fig. 7A,B): Valva very broad basally, strongly tapered apically, sacculus bifurcate, dorsal arm often slightly longer than ventral arm, both relatively short; tegumen narrow, uncus small; socii and gnathos thin; phallus heavily sclerotized, pistol-shaped, long, thin, shaft often slightly curved, with a characteristic long, thin projection at tip, usually directed downwards about 45°, emanating from right-hand side phallus wall (looking toward tip), but twisting slightly to more or less centre, base of projection about twice as broad as tip; lateral ridge along apical third of shaft on left, shaft broader at tip, dorsally rather flat, broad V-shaped keel ventrally.

♀ **genitalia** (Fig. 8A-C): Lamella antevaginalis almost reaching end of antrum, ostium bursae and antrum heavily sclerotized, rather straight, bifurcate, dorsally broader, parallel sided with rounded base and ventrally acutely pointed, leading to blind membranous pouch; ductus bursae short, emanating dor-

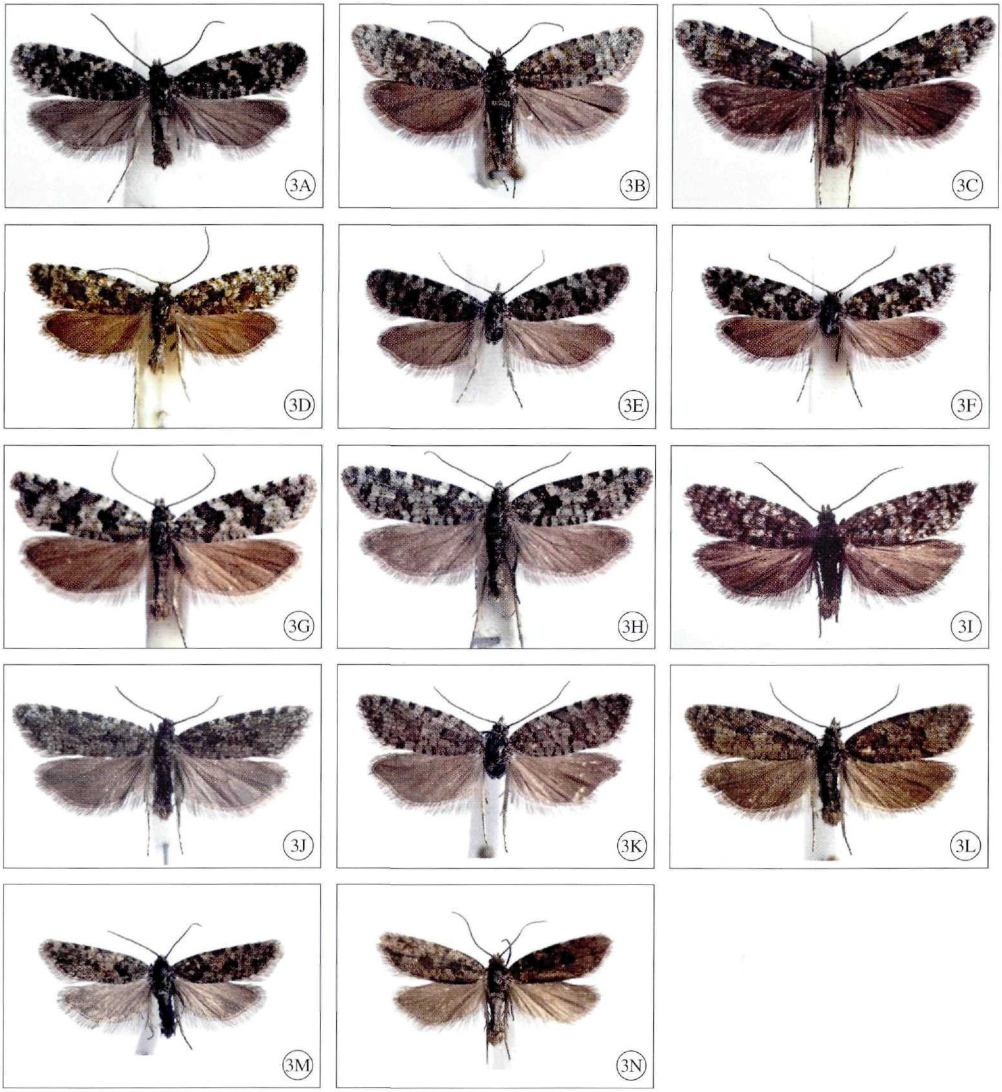


Fig. 3: Adult males of *Sphaleroptera* species. **A** – *S. a. alpicolana* Switzerland: Valletta da Bever, GR, 2320m, e.p. *Silene acaulis* 14.7.2000; **B** – *S. a. alpicolana* Germany: Südbayern, Karwendel M.7.77 1900m, Fr.Zürnbauer; **C** – *S. a. buseri* Switzerland: Täschalp, VS, 2580m, 14.7.1990, S.E.Whitebread (Holotype); **D** – *S. a. buseri* Switzerland: Täschalp, VS, 2580m, 14.7.1990, S.E.Whitebread; **E** – *S. occidentana* Switzerland: Gr. St. Bernhard, 2500m, 26.7.1989, H. Buser; **F** – *S. occidentana* Switzerland: Schwarzsee, VS, 2580m, 23.7.1984, S.E.Whitebread (Holotype); **G** – *S. adamelloi* Italy: Adamello, Mandron 2500m 7.–10.7.1964, leg. K.Burmann; **H** – *S. adamelloi* Italy: Adamello, Rif. Mandron 2700m M.8.58, leg. K.Burmann (Holotype); **I** – *S. orientana* Austria: Styria, Höchstein, Lorbruk [?], 31/7/10, 2200m; **J** – *S. orientana* Austria: Osttirol, Schobergr., Alkuser Scharte, 2630m 8.8.1988 / leg. Tarmann; **K** – *S. o. suborientana* Italy: Südtirol, 2050m, Sella-Gruppe, SO Grödnerjoch, 11.8.1991, leg. Huemer (Holotype); **L** – *S. o. suborientana* Italy: Südtirol, 2050m, Sella-Gruppe, SO Grödnerjoch, 11.8.1991, leg. Huemer; **M** – *S. dentana* Austria: Osttirol 2400m, Schobergruppe, Hochschober Hütte S. Nase, 1.9.1991, leg. Tarmann (Holotype); **N** – *S. dentana* Austria: Osttirol 2960-3030m, Granatspitzgruppe, Wallach Köpfe, 15.8.1991, leg. Tarmann

sally from antrum, ductus seminalis leading from beginning of ductus bursae dorsally; corpus bursae short, about as long as antrum, signum absent.

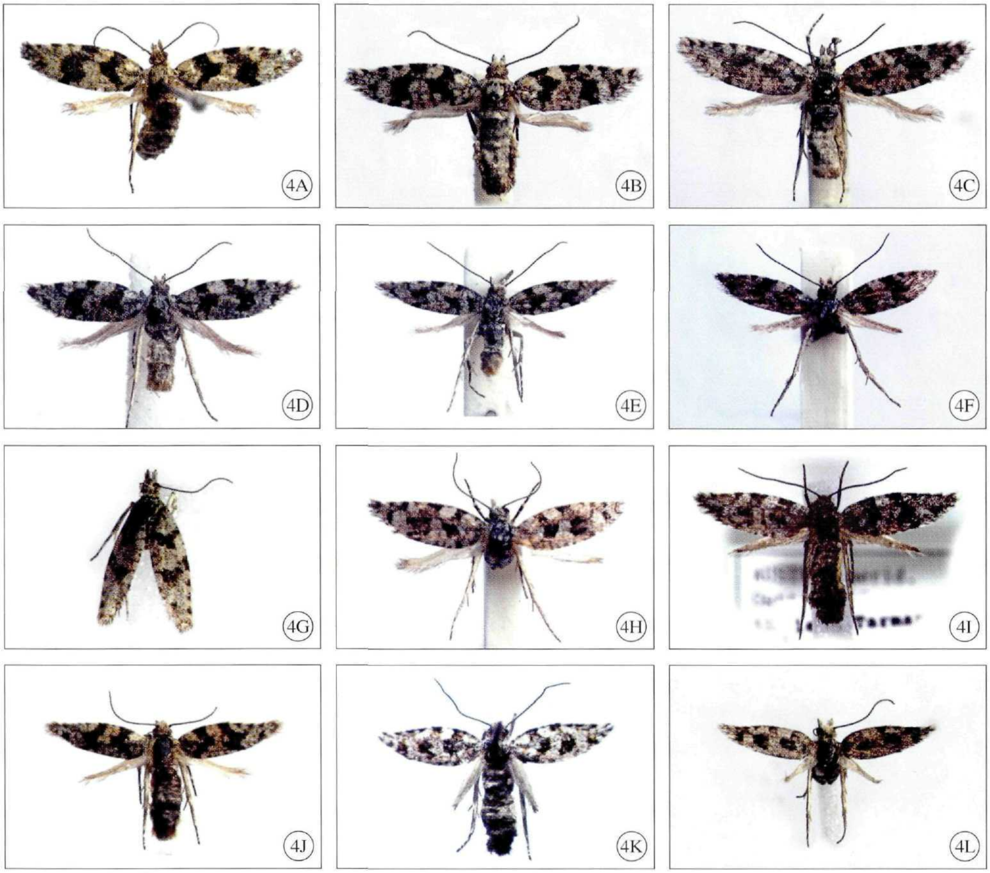
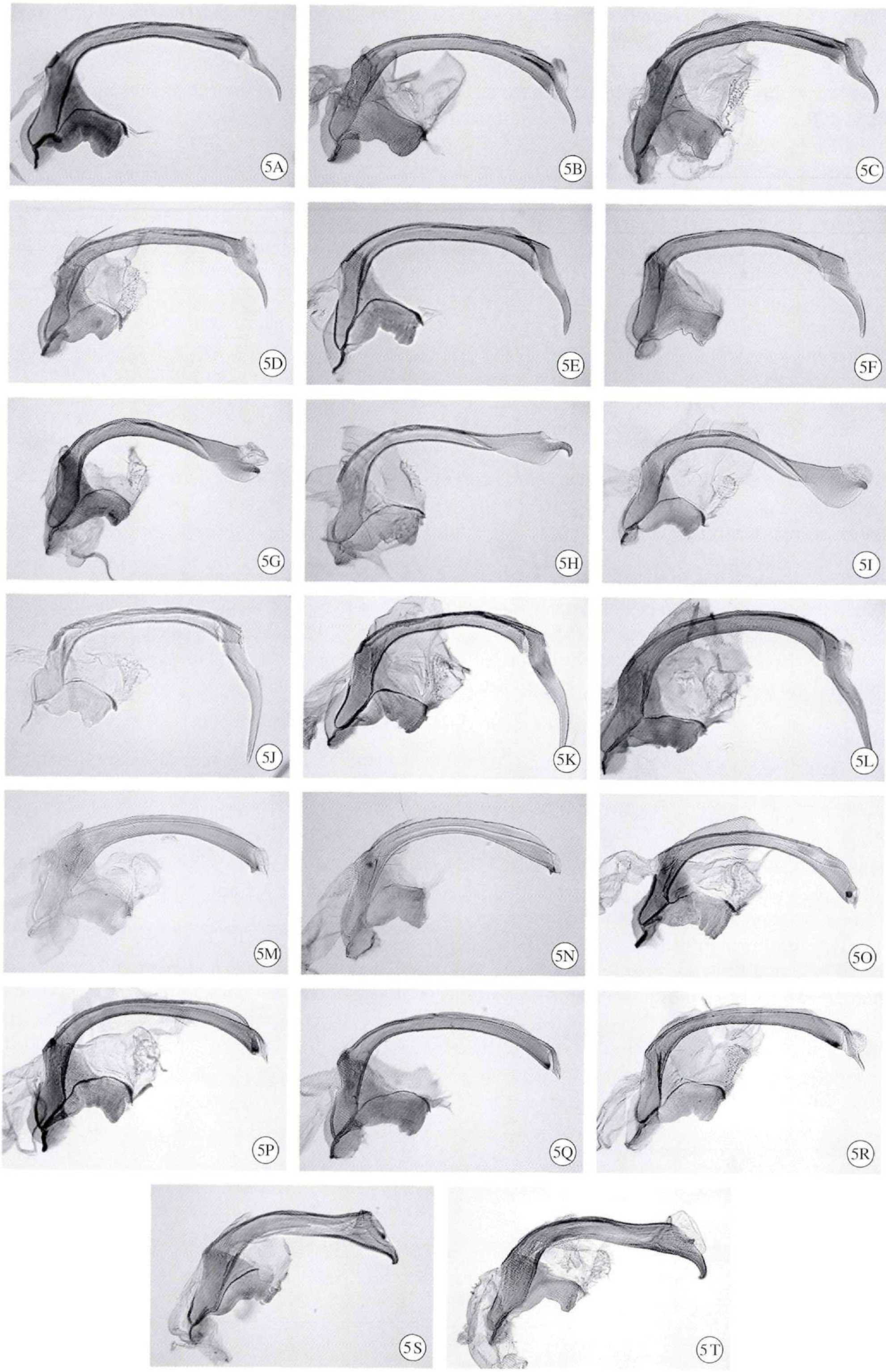


Fig. 4: Adult females of *Sphaleroptera* species. **A** – *S. a. alpicolana* Austria: Tirol, Sattelspitzen, 2200m 15.7.1947, leg. Kappeller; **B** – *S. a. alpicolana* Austria: Tirol, Rettenbachtal 2500m 31.7.1950, leg. Kappeller; **C** – *S. a. alpicolana* Austria: Nord Tirol, Mandl Spitze 2300m 10.8.1971, leg. Kappeller; **D** – *S. a. alpicolana* Switzerland: Valletta da Bever, GR, 2320m, e.p. *Silene acaulis* 14.7.2000; **E** – *S. a. buseri* Switzerland: Täschalp, VS, 2850m, 13.8.1988, S.E.Whitebread; **F** – *S. occidentana* Switzerland: Schwarzsee, VS, 2580m, 23.7.1984, S.E.Whitebread; **G** – *S. occidentana* France: Alpes de Haute Provence, SW Castel du Restford, Ste. De Ceire Brun N. Flanke, 2420m, 26.7.1990, leg. Huemer + Tarmann; **H** – *S. adamelloi* Italy: Adamello, Mandron, 2800m 30.7.-1.8.1964, leg. K. Burmann; **I** – *S. orientana* Austria: Osttirol, Schobergr., Alkuser Scharte, 2630m 8.8.1988, leg. Tarmann; **J** – *S. orientana* Austria: Osttirol 2680-2720m, Schobergruppe, Mischach Scharte, 2.9.1991, leg. Tarmann; **K** – *S. dentana* Led. Glok., 1861; **L** – *S. dentana* Austria: Osttirol 2760-2880m, Schobergruppe, Bawenek Scharte E., 29.8.1991, leg. Tarmann.

Fig. 5: Male genitalia of *Sphaleroptera* species: Phalli. **A** – *S. a. alpicolana* Switzerland: Soglio, Duan, GR, 2600m, 27.8.1981, S.E.Whitebread, GP 405; **B** – *S. a. alpicolana* Switzerland: Sardonna, SG, 3.viii.04, leg J. Müller-Rutz, GP E435; **C** – *S. a. alpicolana* Switzerland: Mattmark, VS, 24.VII.1923, Coll. Dr. G. Audéoud, GP E612; **D** – *S. a. buseri* Switzerland: Augstbordpass, VS, 14.VIII.1903, Coll. Dr. G. Audéoud, GP E609; **E** – *S. a. buseri* Switzerland: Täsch-Alp, VS, 10.8.1982, H. Buser, GP E335; **F** – *S. a. buseri* Switzerland: Col du Pigne, VS, 3300m, 23.7.1983, S.E.Whitebread, GP E434; **G** – *S. occidentana* Switzerland, Schwarzsee, VS, 2580m, 23.7.1984, S.E.Whitebread, GP 469 (Holotype); **H** – *S. occidentana* France: Mont-Gelas, 28.vii.1923, Dr. E. Wehrli, GP E423; **I** – *S. occidentana* Italy, Val Soana, Arietta m 2500 – 8,926, G Della Beffa, GP E475; **J** – *S. adamelloi* Italy: Mt.Adamello, Rif. Garibaldi, 2550m, 1938.viii.4-8, Schmidt, GP E472; **K** – *S. adamelloi* Italy: Adamello E.8.79, 2580m, Fr.Zürnbauer, GP E526; **L** – *S. adamelloi* Italy: M. Piano, 1876, Mann, GP E606; **M** – *S. o. orientana* Austria: Osttirol, Schobergr., Alkuser Scharte, 2630m, 10.8.1988, leg. Tarmann, GP E524 (Holotype); **N** – *S. o. orientana* Austria: Carinthia, Gross Glockner, f. 23.vii.93, Coll. Krone, GP E471; **O** – *S. o. orientana* Austria: Warscheneck, Ob-Öst., 7.8.02, GP E530; **P** – *S. o. suborientana* Italy: Südtirol, 2050m, Sella-Gruppe, SO Grödnerjoch, 11.8.1991, leg. Huemer, GP E614 (Holotype); **Q** – *S. o. suborientana* Italy: Prov. Udine, Alpi Giulie, Rif. Gilberti 2050m, 3.8.1987, leg. Huemer, GP E504; **R** – *S. o. suborientana* Italy: Rosengarten, A.9.71, 2100m, Fr.Zürnbauer, GP E503; **S** – *S. dentana* Austria: Styrie, leg. L. Paravicini, GP E441; **T** – *S. dentana* Italy: Mont Piano 1876, Schludebach, coll. Mann, GP E605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Larva: The larva has not been described, but from a parasitized larval skin, the head appears to be brown and the plate dark brown or black.
Pupa (Fig. 9): Two strong anal spines pointing dorsally. Abdominal segments with dorsal rows of many rearward pointing short spines, on rear and front edges of segments 2–6, on front edge only on segments 7 and 8. Rows on front edge always more prominent. A row of setae on segment 9.

Life history and biology

Adults start to emerge mid-July, peaking in August, but depending on local conditions can emerge earlier and continue into September; extreme dates: 26th Jun-15th Sep.
The larva has only rarely been found and it has not been described. BURMANN (1958) reports having found pupae under rocks and having bred specimens from larvae found more or less accidentally. The author has also found pupae in larval spinnings in *Saxifraga oppositifolia* cushions and in silken cocoons under adjacent rocks below the Forcellina Pass in Grisons, Switzerland. Many ichneumonid wasp cocoons were found in the same spinnings. In Val Bever, Grisons, several pupae were found in larval spinnings among cushions of *Silene aucaulis*. They were situated vertically, just below the surface of the cushion. These two plants are thereby confirmed as larval foodplants. Indeed, they characterize the typical habitat of the species. Above Siat, Grisons, however, the males have been found very commonly in an area where neither of these foodplants appeared to be present.

Distribution (Fig. 10)

Widespread in a broad band across the central part of the Alpine arch, from the Saas valley of Switzerland in the southwest to southern Bavaria (Germany) in the northwest, including South Tyrol (northern Italy), but apparently rare east of Bolzano, and North Tyrol in Austria. Altitudinal range: 1,900–3,400m (median 2,545m).
One specimen labelled 'Schneeb' probably refers to the locality 'Schneeberg' (but possibly also to a collector's name). At least three Schneebergs exist in the Alps: south west of Vienna in Lower Austria, west of St. Johan in Salzburg and north of Merano in South Tyrol, Italy. The latter is considered the most likely, both because it fits better with the known distribution of *alpicolana*, because of its much higher altitude and the fact that the specimen was deposited in an Italian museum (Milan).

Remarks

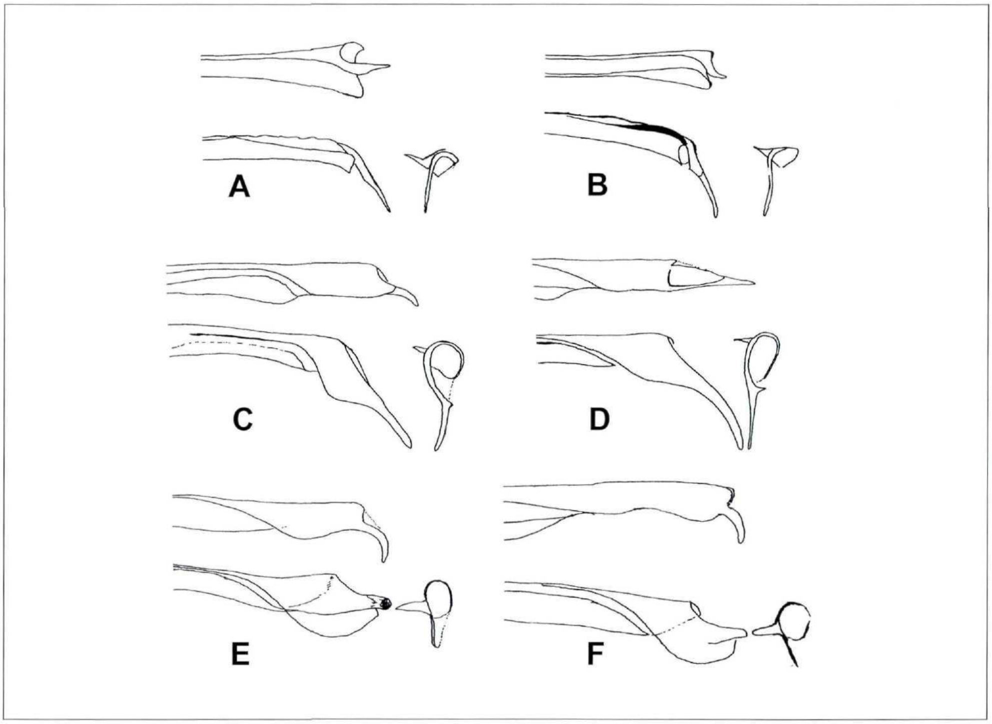
This species is very variable and six forms (denoted by the letters A to F) were recognised by BURMANN (1958). He gave infrasubspecific names to two of these: a dark unicolorous f. *obscurana* (form D) and a pale form, f. *pallidana* (form E). At that time, Burmann only had material from the region around Innsbruck and the Ötztal Alps, Austria, where only *S. alpicolana* s.str. is known to fly. He noted that those populations occurring on calcareous rocks tended to be lighter than those on siliceous rocks, although all forms could occur among any population. These individual forms are not restricted to *S. a. alpicolana*, but are found in most *Sphaleroptera* species.
The type locality of Frölich's *alpicolana* is the Allgäu Alps of southern Bavaria, Germany. No specimens could be found from this area to demonstrate that they actually belong to *S. a. alpicolana*, as defined here. However, of all the known *Sphaleroptera* species, the distributional range of *S. a. alpicolana* fits best with an occurrence in the Allgäu Alps. It occurs further east in Bavaria (Karwendel) and across the border in Austria, both in North Tyrol and in Vorarlberg. The existence of an as yet undescribed *Sphaleroptera* species in southern Germany would seem unlikely, as no Alpine endemics are known from this area (HUEMER 1998).

***Sphaleroptera alpicolana buseri* ssp.n.**

Euledereria alpicolana sensu OBRAZTSOV 1955, ♀ genitalia Fig. 314.

Material examined: 56♂,7♀

Holotype: 1♂, 'VS Schweiz, Täschalp, 2580m, 629.9/101.5, 14.7.1990, S.E.Whitebread' 'Holotype' [NHMB] – **Paratypes: Switzerland:** 1♂, Zermatt, Suisse, 7 1890, Ch. Blachier [MHNG]; 1♂, alpi-



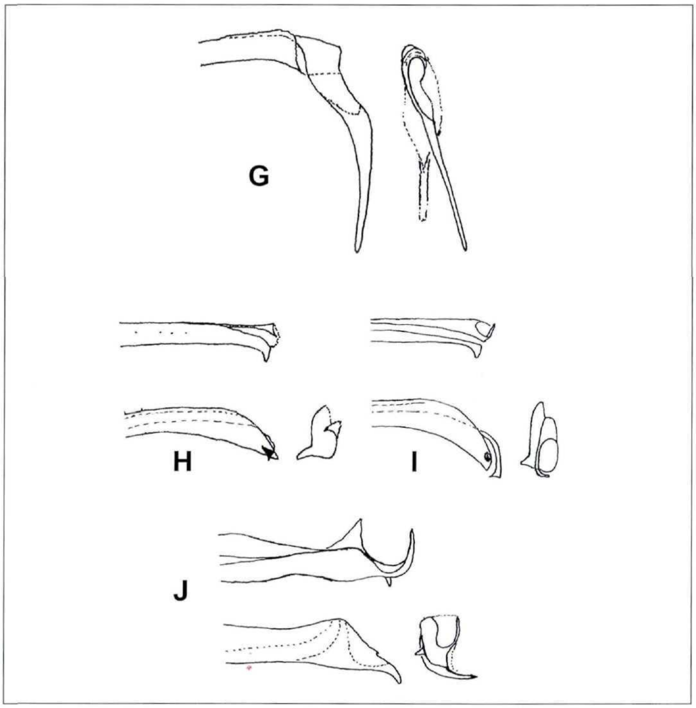


Fig. 6: Male genitalia of *Sphaleroptera* species: Phallus tips drawn from dorsal, lateral and frontal aspects. **A** – *S. a. alpicolana* Switzerland: Ebenalp, AI, m vii.89, leg. J. Müller-Rutz, GP E430; **B** – *S. a. alpicolana* Switzerland: Sirwoltesee, VS, 2230m, 12.8.1984, S.E.Whitebread, GP 453; **C** – *S. a. buseri* Switzerland: Mettelhorn, VS, 3300m, 1.8.1981, S.E.Whitebread, GP 346; **D** – *S. a. buseri* Switzerland: Gornergrat, VS, 3000m,13.9.69, Coll. E. de Bros, GP E416; **E** – *S. occidentana* Switzerland: Zermatt, Alp Hermettji, 2000-2500m, 20.8.1978, S.E.Whitebread, GP 345; **F** – *S. occidentana* Switzerland, Schwarzsee, VS, 2580m, 23.7.1984, S.E.Whitebread, GP 469 (Holotype); **G** – *S. adamelloi* Italy: Mt.Adamello, Rif. Garibaldi, 2550m, 1938.viii.4-8, leg. Schmidt, GP E472; **H** – *S. o. orientana* Austria: Carinthia, Gross Glockner, f. 23.vii.93, Coll. Krone, GP E471; **I** – *S. o. suborientana* Italy: Venezia Tridentina, Val di Marebbe, Fanes Pico m. 2100, 10.vii.931, L. Rocca legit, Coll. Della Beffa, GP E476; **J** – *S. dentana* Austria: Styrie, leg. L. Paravicini, GP E441.

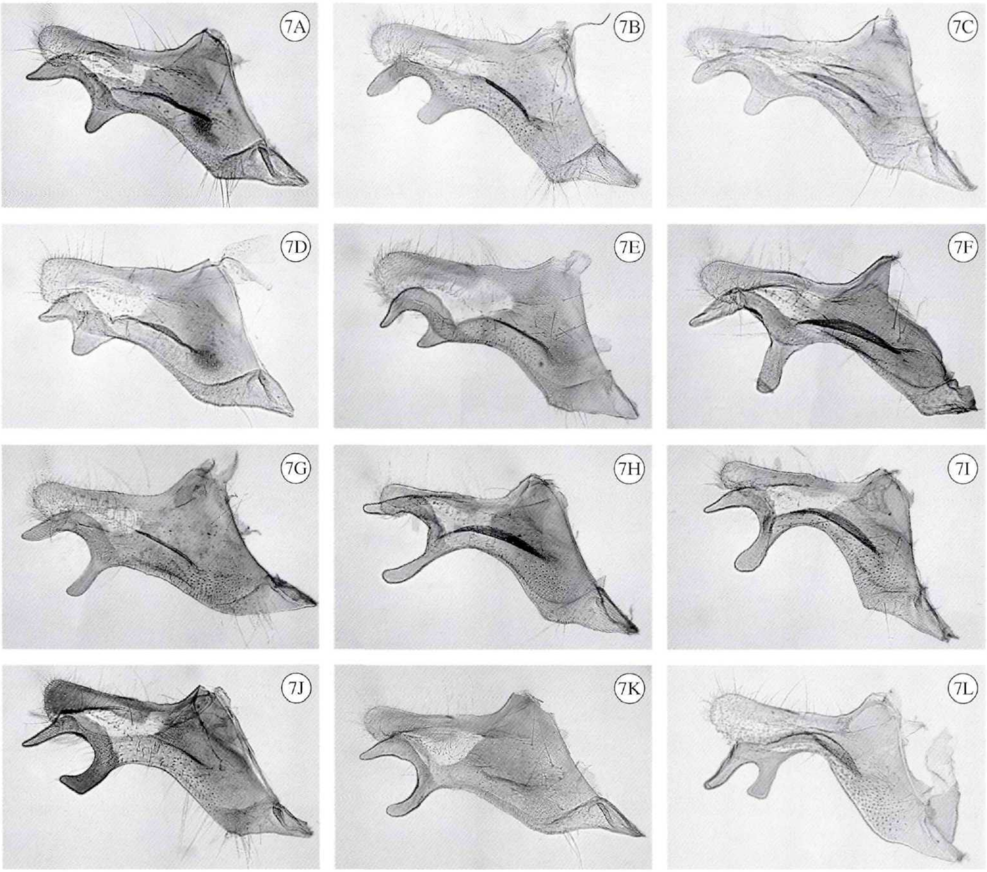


Fig. 7: Male genitalia of *Sphaleroptera* species: Left-hand valvae. **A** – *S. a. alpicolana* Italy: Nord Tirol, Stubaital Schrankogl, 3400m, 15.9.1970, Burmann, GP E608; **B** – *S. a. alpicolana* Switzerland: Mattmark, VS, 24.VII.1923, Coll. Dr. G. Audéoud, GP E612; **C** – *S. a. buseri* Switzerland: Augstbordpass, VS, 14.VIII.1903, Coll. Dr. G. Audéoud, GP E609; **D** – *S. occidentana* Switzerland: Gr. St. Bernhard, 2500m, 26.7.1989, H. Buser, GP E502; **E** – *S. occidentana* Italy, Val Soana, Arietta m 2500 – 8,926, G Della Beffa, GP E475; **F** – *S. adamelloi* Italy: Adamello E.8.79, 2580m, Fr.Zürnbauer, GP E526
G – *S. adamelloi* Italy: M. Piano, 1876, Mann, GP E606; **H** – *S. o. orientana* Austria: Warscheneck, Ob-Öst., 7.8.02, GP E530; **I** – *S. o. orientana* Switzerland: leg. Staudinger, GP E611; **J** – *S. o. suborientana* Italy: Südtirol, 2050m, Sella-Gruppe, SO Grödnerjoch, 11.8.1991, leg. Huemer, GP E614; **K** – *S. o. suborientana* Italy: Rosengarten, A.9.71, 2100m, Fr.Zürnbauer, GP E503; **L** – *S. dentana* Italy: Mont Piano 1876, Schludebach, coll. Mann, GP E605

colana, Gornergrat m 2.viii.34, J. Müller-Rutz [NHMB] GP E.443; 1♂, Gornergrat VS 3000m 13.9.69, E. de Bros, [coll. S. Whitebread, KML]; 1♂, Gornergrat VS 3000m 13.9.69, E. de Bros [coll. S. Whitebread, KML] GP E.415; 1♂, Gornergrat VS 3000m 13.9.69, E. de Bros [coll. S. Whitebread, KML] GP E.416; 1♂, Gornergrat VS 3000m 13.9.69, E. de Bros [coll. S. Whitebread, KML] GP E.417; 2♂, Gornergrat, 2.viii.34, 11864 m, P.Weber, [ETHZ]; 1♂, Helvetia, Riffelberg, 9.8.1982, H. Buser, [coll. S. Whitebread, KML] GP 2; 4♂, Riffelalp, 26.vii.28, 10037 m, P.Weber [ETHZ]; 3♂, Wallis Helvetia, Täsch-Alp, 10.8.1982, H. Buser, 3000m [coll. S. Whitebread, KML] GP E.335; 1♂, Wallis Helvetia, Täsch-Alp, 10.8.1982, H. Buser [coll. S. Whitebread, KML]; 1♂, Wallis Helvetia, Täsch-Alp, 10.8.1982, H. Buser, 2900m [coll. S. Whitebread, KML] GP E.550; 1♂, Wallis Helvetia, Täsch 3250m, 2.8.1984, H. Buser, [coll. S. Whitebread, KML] GP E.439; 3♂, Wallis Helvetia, Täsch 2850m, 2.8.1984, H. Buser [coll. S. Whitebread, KML]; 1♂, Wallis Helvetia, Täsch 2850m, 7.8.1984, H. Buser [coll. S. Whitebread, KML]; 1♀, VS Schweiz, Täschalp, 2850m, 13.8.1988, S.E. Whitebread [coll. S. Whitebread, KML]; 1♂, VS Schweiz, Täschalp, 13.8.1988, S.E.Whitebread, 3250m [coll. S. Whitebread, KML]; 2♂, Wallis Helvetia, Täsch-Alp, 2900[m], 4.8.1989, H. Buser, [coll. S. Whitebread, KML]; 2♂, VS Schweiz, Täschalp, 14.7.1990, S.E.Whitebread, 2580m [coll. S. Whitebread, KML]; 1♀, VS Schweiz, Täschalp, 3250m, 10.8.1991, H. Buser [coll. S. Whitebread, KML]; 1♀, alpicol., Schönbiel, f 19.vii.24, J. M.-R. [NHMB] GP E.436; 1♀, alpicolana, Triftkummen, f 30.VII.34 W[eber], [NHMB] GP E.437; 2♂, Zermatt, Triftkummen, 30.vii.34, 11851 m, P.Weber [ETHZ]; 2♂, Zermatt, Triftkummen, 7.8.23 and 24.7.28 [NHMBe]; 1♂, Mettelhorn – Trift, 3200me 5.viii.1920, Dr. E. Wehrli [NHMB]; 1♂, Mettelhorn, 3200m 24.vii.1920, Dr. E. Wehrli [NHMB] GP E.440; 1♂, Mettelhorn – Trift, c.3200 5.viii.1920, Dr. E. Wehrli [Coll. J. Müller-Rutz, NHMB]; 1♂, VS Schweiz, Mettelhorn, 3300m, 1.8.1981, S.E.Whitebread [coll. S. Whitebread, KML] GP 346; 1♀, VS Schweiz, Mettelhorn, 3400m 623.4/100.5, Bred 16.8.1981, S.E.Whitebread, ex larva in silken tube amongst *Saxifraga oppositifolia*, taken 1.8.1981 [coll. S. Whitebread, KML] GP 585; 1♂, Helvetia, Mettelhorn, 3380[m] 12.8.1982, H. Buser [coll. S. Whitebread, KML]; 1♂, Helvetia, Mettelhorn Gipfel, 12.8.1982, H. Buser, S. Whitebread [coll. S. Whitebread, KML] GP 1; 1♀, VS Schweiz, Mettelhorn, 3400m 623.35/100.5, Bred 12.8.1984, S.E.Whitebread, ex larva in spinning on *Saxifraga oppos*. taken 21.7.1984 [coll. S. Whitebread, KML] GP 452; 1♀, VS Schweiz, Mettelhorn, Bred 17.8.1984, S.E. Whitebread, 3400m 623.35/100.5, ex larva in spinning on *Saxifraga oppos*., taken 21.7.1984 [coll. S. Whitebread, KML] GP 470; 1♂, Trifthorn 3500m 7.viii.1920, Dr. E. Wehrli [NHMB]; 1♂, Trifthorn 3500m 7.viii.1920, Dr. E. Wehrli [NHMB] GP E.424; 3♂, Zinalrothorn Grat 2.viii.20 3400m Dr. E. Wehrli [Coll. J. Müller-Rutz, NHMB]; 1♂, Schalliberg, Weisshornhutte, 6.VIII.1938, coll. M. Rehfous [MHNG]; 2♂, Crêtes de Plumatt, 2.IX.03 [MHNG]; 1♂, Frilithäli, 4.IX.1903, Coll. Dr. G. Audéoud [MHNG]; 1♂, Thounot, 11.VIII.1908, G. Audéoud [MHNG]; 1♂, Schweiz: Valais/Wallis: Ergisch (Turtmanntal), Grubenalp, Grüobtälli 2300–2700m 623/117; 20.07.2005 [coll. P. Sonderegger]; 1♂, Schweiz: Valais/Wallis: Oberems (Turtmann), Gigigrat 2750–2900m 622/116; 22.07.2004 [coll. P. Sonderegger]; 1♂, Augstbordpass, 14.VIII.1903, Coll. Dr. G. Audéoud [MHNG] GP E.609; 1♂, Bella Tola, 29.VII.1903, Coll. Dr. G. Audéoud [MHNG]; 1♂, VS Schweiz, Col du Pigne, 23.7.1983, S.E.Whitebread, 3300m [coll. S. Whitebread, KML] GP 434;1♂, 1692 Wallis m d'R [de Rougemont] [Coll. J. Müller-Rutz, NHMB] GP E.433; 2♂, Vall. 229 3/3, [ETHZ]..

Other material: 1♂, Sphaleroptera alpicolana [no other label] [MHNG].

Description and diagnosis:

Wingspan: males 14.5–20.5mm, median 17.0 mm, n=54; females 13.5–14.5 mm, median 14.0 mm, n=7

Male (Fig. 3C,D): Very variable, general pattern not distinguishable from *S. alpicolana*; ground colour from very pale whitish-grey to dark steely blue-grey, fasciae sometimes not well defined due to more extensive ground colour, fasciae sometimes dark, strongly contrasting with whitish-grey ground colour, sometimes orange scales strongly present.

Female (Fig. 4E; Fig. 2B): The few known specimens are typical *Sphaleroptera* type: pale ground colour strongly contrasting with two dark fasciae. On average, slightly smaller than *S. a. alpicolana* females.

♂ genitalia (Fig. 5D-F; Fig. 6C,D; Fig. 7C): Similar to *S. a. alpicolana*, but projection at tip of phallus thicker, base considerably broader (approx. 3-fold), rolling round to form right-side wall of shaft, left-side wall correspondingly reduced, but lateral ridge still present; dorsally and ventrally more rounded; sacculus similar to *S. a. alpicolana*.

♀ genitalia (Fig. 8D-F): Ostium bursae as wide or wider than in *S. a. alpicolana*, antrum heavily sclerotized, generally shorter than in *S. a. alpicolana*, clearly bifurcate, dorsally more or less straight, ventrally strongly curved to right at tip acutely pointed, leading to moderately large membranous pouch; ductus bursae short, as in *S. a. alpicolana*.

Pupa: Similar to that of nominate subspecies.

Derivatio Nominis

Named after my good friend the late Heinz Buser, who had a great affinity for the region in which this species flies and who was instrumental in bringing the '*alpicolana*' problem to my attention.

Life history and biology

Adults start to emerge mid July, peaking in August, but depending on local conditions can continue into September; extreme dates: 14th Jul-13th Sep. Larvae have been found on two separate occasions on the summit of the Mettlelhorn, near Zermatt, Switzerland (3,400m) feeding from silken tubes spun among clumps of *Saxifraga oppositifolia* (Fig. 1A,F). This is probably the main foodplant of this subspecies.

A female *buseri* bred from one of these larvae on 12th Aug. 1984 was presented to a male *S. a. alpicolana* taken on the Nufenen Pass (Ticino, Switzerland) at 08.45h the same day. They were placed together the following evening in a large plastic box placed under a lamp. The male first began to probe damp soil with its proboscis, but within 10 minutes had mated with the female. The mating lasted about 1.5 hours. The female lived another two weeks and a few eggs were laid on a rock. These appeared to have been fertilized as they coloured up, but they did not hatch that autumn, and the material was accidentally lost during the winter.

Distribution (Fig. 10)

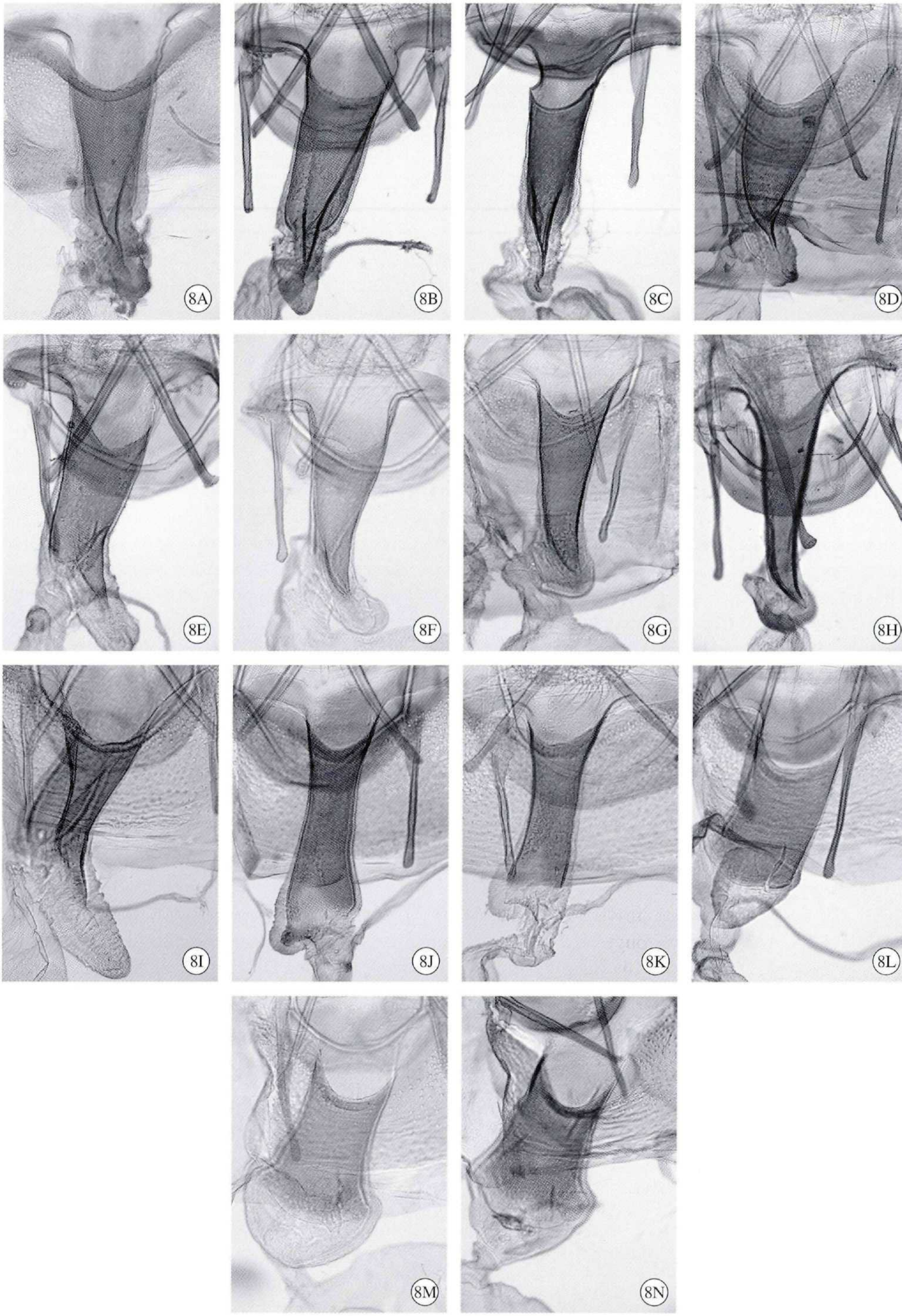
The subspecies occurs only in a small area of the Valais of Switzerland west of the mountain range dividing the Saas and Matter valleys and north of the Gorner Glacier in Zermatt (Fig. 1D), south of the Rhone valley and westwards to at least the Val d'Anniviers (Val de Moiry). The situation further west is not known. Altitudinal range: 2,540–3,500m.

Its distributional range is partly sandwiched between that of *S. occidentana* and *S. a. alpicolana*. However, none of these three taxa appear to occur sympatrically. *S. a. buseri* is separated from *S. a. alpicolana* by the high alpine ridge between the Matter and Saas valleys, which includes some of the highest Alpine peaks, such as the Täschhorn (4,491m) and Dom (4,545m). Furthermore, on the Saas side, the glaciers extend very low, to about 2400m. Around Zermatt, *S. a. buseri* is separated from *S. occidentana* by the Gorner and Zmutt Glaciers. The narrowest distance between populations of these two taxa is probably only 1.5 –2 km. *S. a. buseri* also tends to fly much higher than either *S. occidentana* or *S. a. alpicolana*. The medians of the altitudinal ranges of the studied material are: *occidentana*: 2,650m (n=19); *buseri*: 3,000m (n=41); *alpicolana*: 2,545m (n=71). No specimens are known from the area where these three taxa appear to join, i.e. in the triangle formed by Gornergrat, Monte Rosa and Mattmark. This area is largely composed of glaciers and permanent snowfields, but suitable *Sphaleroptera* habitat should also be present.

Remarks

Based on the apparently successful mating of a female *buseri* and a male *alpicolana*, this taxon is provisionally considered to be a subspecies of *S. alpicolana*, rather than a full species. The result of this mating could not be followed through, so if the progeny was not viable, a specific status could be considered. As mentioned above, the distributions of the two subspecies almost meet in the region around Saas Fee and Täsch in the Valais of Switzerland, but are probably sufficiently isolated from one another to make a chance mating between the two taxa to be a very rare occurrence. This could only occur if a male

Fig. 8: Female genitalia of *Sphaleroptera* species: Detail of antrum, ostium bursae and ductus bursae. **A** – *S. a. alpicolana* Austria: Nord-Tirol, Acherkogel, 7.8.28, Zerny leg, GP 10851 (Razowski); **B** – *S. a. alpicolana* Switzerland: Sardonna, SG, 30.VII.18, GP E438; **C** – *S. a. alpicolana* Austria: Tirol, Samoar Hütte ca. 3000m, 23.7.1950, Kappeller, GP E610; **D** – *S. a. buseri* Switzerland: Mettelhorn, VS, 3400m, e.l. *Saxifraga oppos.* 12.8.1984, S.E.Whitebread, GP 452; **E** – *S. a. buseri* Switzerland: Schönbiel, VS, f 19.vii.24, GP E436; **F** – *S. a. buseri* Switzerland: Triftkummen, VS, f 30.VII.34, leg. Weber, GP E437; **G** – *S. occidentana* Switzerland: Schwarzsee, VS, 2580m, 23.7.1984, S.E.Whitebread, GP 455; **H** – *S. occidentana* France: Alpes de Haute Provence, SW Castel du Restford, Ste. De Ceire Brun N. Flanke, 2420m, 26.7.1990, leg. Huemer + Tarmann, GP E603; **I** – *S. adamelloi* Italy: Adamello, Mandron 2800m, 30.7.-1.8.1964, leg. K. Burmann, GP E522; **J** – *S. o. orientana* Austria: Osttirol, Schobergr., Alkuser Scharte, 2630m, 8.8.1988, leg. Tarmann, GP E527; **K** – *S. o. orientana* Austria: Schober-Gr., 2200m, 28.vii.1923, Coll.R.Kitschelt, GP E529; **L** – *S. dentana* Italy: Mont Piano, 1876, Schudebach, coll. Mann, GP E525; **M** – *S. dentana* Austria: Glockn., Mann, GP E531; **N** – *S. dentana* Austria: Osttirol 2760–2880m, Schobergruppe, Bawenek Scharte E., 29.8.1991, leg. Tarmann, GP E613.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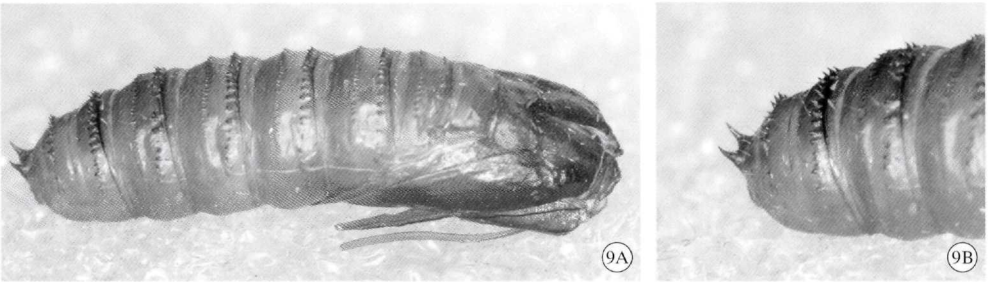

Fig. 9: Pupa of *Sphaleroptera alpicolana* (female), **A** – Exuvia; **B** – detail of cremaster. Switzerland, Bever, GR, July 2000.

is blown across the high mountain range separating the two populations. Females, especially gravid females, are very unlikely to be able to achieve this. Even males would not be very prone to being swept up by the wind, as they only fly in sunshine and more usually during the early morning hours – conditions when strong winds are not usual. *S. a. buseri* appears to lie morphologically between *S. a. alpicolana* and *S. occidentana* and could have originated as a true hybrid between these two species, or corresponding earlier forms. From the current distribution and the fact that the altitudinal range of *buseri* extends higher up than either of the other two species, it is considered very likely that during the Pleistocene ice ages it survived on the highest peaks of the region of Zermatt that rose above the ice (nunataks), whereas *S. a. alpicolana* and *S. occidentana* were displaced to separate peripheral refugia. This could have happened at each of the glacial maxima over the last hundreds of thousands of years. Gene flow between these taxa may have only been possible during the warmest interglacial periods. Effective isolation could have existed for tens of thousands of years between each of these periods.

***Sphaleroptera occidentana* sp.n.**
Sphaleroptera alpicolana var. *lugubrana* DELLA BEFFA 1934:94

Material examined: 26♂,2♀

Holotype: 1♂, 'VS Schweiz, Zermatt, Schwarzsee, 2580m, 620.85/093.2, 23.7.1984, S.E.Whitebread' 'Holotype' 'S.E.W. GP No. 469 ♂ ' [NHMB] – **Paratypes: France**: 1♂, Pyrenees cent.: Pic du Midi de Bigorre 2650m, 4.viii.1981, Sattler, Tuck & Robinson BM1981–383 [BMNH]; 1♂, Pyrenees cent.: Pic du Midi de Bigorre 2650m, 4.viii.1981, BM.GP.23385 / Sattler, Tuck & Robinson BM1981–383 [BMNH]; 1♂, Mont-Gelas, 28.vii.1923 a.m., 3000–3150[m], Dr. E. Wehrli [coll. J. Müller-Rutz, NHMB] GP E.423; 1♀, Frankreich, Dep. Alpes de Haute Provence, SW Castel du Restford, Ste. De Ceire Brun N. Flanke, 2420m 26.7.1990, leg. Huemer & Tarmann, [TLMF] GP E.603;1♂, Aiguille Bocher, 2500m, 8.viii.31, leg. Berthet [coll. Réal]; 3♂, Aiguille Bocher, 27 à 2800m, 8.viii.31, leg. Berthet [coll. Réal]; 1♂, Pralognpass [?], 2800m, Aig-Bocher, 8.viii.31, leg. Berthet [coll. Réal]; 1♂, Banteleina, 2680m, 30.ix.31, leg. Berthet [coll. Réal]; 1♂, Face S. Pelvoux 2'750 [coll. Réal]; 3♂, Savoie, Bonneval-s/Arc (L. Viard) 24.vii.1912, [coll. H.Legrand, MNHP] – **Italy**: 1♂, Alpi Occ., Val Soana, Arietta m 2500 – 8,926, G Della Beffa [MCSN] GP E.475; 1♂, Cima di Argentera, 31.vii.1923, Dr. E. Wehrli, [NHMW]; 1♂, It.s.Alagna, leg. Preissecker, [NHMW]; 1♂, M. Camoscio, 4.8.06 (29), M.Rosa, 11077, [NHMW] – **Switzerland**: 1♂, Helvetia, Gr. St. Bernhard, 2500m, 26.7.1989, H. Buser [coll. S. Whitebread, KML] GP E.502; 1♂, VS Schweiz, Zermatt, Trockenersteg, 2860m, 10.9.1978, A.Bentley [coll. S. Whitebread, KML] GP 344; 1♂, VS Schweiz, Zermatt, Trockenersteg, 2860m, 10.9.1978, A.Bentley, [coll. S. Whitebread, KML]; 1♀, VS Schweiz, Zermatt, Schwarzsee, 2580m, 23.7.1984, S.E.Whitebread [coll. S. Whitebread, KML] GP 455; 1♂, VS Schweiz, Zermatt, Alp Hermettji, 2000–2500m, 20.8.1978, S.E.Whitebread, [coll. S. Whitebread, KML] GP 345; 1♂, VS Schweiz, Zermatt, Alp Hermettji, 2000–2500m, 20.8.1978, S.E.Whitebread, [coll. S. Whitebread, KML].

Other material: France: 3♂, [unlabelled specimens in coll. Réal].

Description and diagnosis:
Wingspan: males 15.5–18.0mm, median 17.0 mm, n=13; female 12.5 mm, n=1
Male (Fig. 3E,F; Fig. 2A): Very variable, pattern otherwise not distinguishable from *S. alpicolana*; ground colour usually steely blue-grey, sometimes only slightly paler than fasciae, giving a dark, poorly contrasting, drab, unicolorous form (f. *lugubrana*), sometimes much paler than fasciae, giving a more contrasting form, with orange scaling.
Female (Fig. 4F,G): Only two specimens available, one very pale and strongly contrasting with dark fasciae, the other is very worn, but appears to have relatively broad fasciae and some bluish scales are present.
♂ genitalia (Fig. 5G-I; Fig. 6E,F; Fig. 7D,E): Similar to *S. a. buseri*, but projection at tip shorter and turned 90° to left (viewed towards tip), base very broad, rounded, lateral ridge displaced back down shaft to about one half causing a widening at this point; ventral arm of sacculus bifurcation often broad triangular.
♀ genitalia (Fig. 8G,H): Ostium bursae broader than in *alpicolana*, antrum heavily sclerotized, generally longer than in *alpicolana*, rather straight, but curved to right at tip, not obviously bifurcate, ventrally acutely pointed, membranous pouch absent; ductus bursae short, possibly slightly broader than in *alpicolana*.

Derivatio Nominis
From the Latin '*occidens*' = west, referring to the western Alpine distribution of the species

Life history and biology
Adults have been found between 23rd July and 30th September. The larva of this species has not been found, but the adult has often been seen around *Silene acaulis* and this is probably a foodplant of the species.
A female was taken 23rd July 1984 at Schwarzsee, below the Matterhorn, Zermatt, Switzerland (Fig. 1C). It used its proboscis to take in water provided on cotton wool. About 30 eggs were laid over the following six days, when the female died. They were laid under a rock, under leaves of *Saxifraga oppositifolia* and on the lid of the plastic container. They were initially yellow and some were loosely covered by particles of sand and anal hairs of the female. They turned reddish after about 2 days and darkened afer 7 days. After 11 days, some eggs were opened and fully developed larvae were released. The remaining eggs hatched naturally one week later. The neonate larvae were reddish with a black head and plate. They did not feed on the provided *Saxifraga*. It is possible that this is not their natural foodplant, or the provided conditions were simply not conducive to feeding. Alternatively, perhaps the young larva hibernates without feeding, or that in the wild, the larvae overwinter fully developed in the egg.

Distribution (Fig. 10)
Occurs in the Pyrenees and the southwestern Alps of France, Italy and Switzerland. Pyrenean specimens have only been seen from the Pic du Midi (Hautes Pyrénées), but LHOMME (1935–1949) reports '*alpicolana*' from both Hautes Pyrénées (Bagnères de Bigorre) and Pyrénées Orientales (Fourmiguères). In Switzerland, the species is known to occur only south of the Gorner and Zmutt Glaciers in Zermatt and west to the Grand St Bernard region. Altitudinal range: 2,420–3,000m.

Remarks
Della Beffa's var. *lugubrana* corresponds to Burmann's f. *obscurana* of *S. alpicolana*.
The fact that *S. occidentana* occurs in both the Alps and the Pyrenees suggests that it must have evolved to its present form before the last time a bridge of alpine habitat existed between the Pyrenees and the Alps. During the Würm ice age maximums about 22k and 150k years ago the glaciated Pyrenees is thought to have been surrounded by arid cold steppe, with *Artemisia* as dominant plant and about 150 km

further north (45°N latitude) this merged into a more tundral steppe landscape with permafrost and very sparse vegetation that stretched to the glaciated Alps (VAN ANDEL & TZEDAKIS 1996; TZEDAKIS et al. 1997). It seems doubtful whether this situation represented suitable and uninterrupted *occidentana* habitat, although the earlier glaciation period appeared to last longer, thereby increasing that possibility. However, according to marine oxygen isotope (MOI) data, the extent of glaciation during earlier glacial maxima, especially those of approximately 340k, 640k and 880k years ago (MOI Stages 10, 16 and 22 respectively), possibly exceeded those of the Würm (GIBBARD & VAN KOLFSCHOTEN 2005). Large glaciation events prior to this do not seem to have existed. Alternatively, sea-level data from the Red Sea suggest that the glaciation of MOI Stage 12 (ca. 450 kyr) may also have been more extensive than the last maximum (ROHLING et al. 1998). Suitable habitat must have reached the Pyrenees during at least one of these periods. It is likely that the Central Massif mountains of France were also colonised by the species at the same time. '*Cnephasia* (*Sphaleroptera*) *alpicolana*' has been reported from this region (RÉAL 1953), but no specimens were found in collections during this study. Only limited Pyrenean material was available, but based on the form of the phallus, there does not seem to be a great difference between the populations closest to *alpicolana* and that from the central Pyrenees. It would appear therefore that gene flow from *alpicolana* to *occidentana* has not occurred since the last time the Alpine and Pyrenean populations became isolated, i.e. for at least 22,000, but more likely several 100 kyr, either due to genetic incompatibility, or to effective isolation. For this reason, *occidentana* is considered a good species.

Sphaleroptera adamelloi sp.n.

Material examined: 7♂,1♀
Holotype: 1♂, 'Italia, Adamello, Rif. Mandron 2700m M.8.58, leg. K.Burmann' 'Holotype' [TLMF] – **Paratypes: Italy:** 1♂, Italia, Adamello, Mandron 2500m 7.–10.7.1964, leg. K.Burmann [TLMF]; ♀, Italia, Adamello, Mandron 2800m 30.7.–1.8.1964, leg. K. Burmann [TLMF] GP E.522; 2♂, Norditalien, Adamello E.8.79 2500m Fr.Zürnbauer [TLMF]; 1♂, Norditalien, Adamello E.8.79 2580m Fr.Zürnbauer [TLMF] GP E.526; 1♂, [Italy] Mt.Adamello, (2550m), Rif. Garibaldi, 1938.viii.4–8, leg. Schmidt [MTMB] GP E.472; 1♂, Mann, 1876, M. Piano [NHMW] GP E.606.

Description and diagnosis:
Wingspan: males 18.0–20.5 mm; median 19.8 mm, n=6; females 14.0 mm, n=1
Male (Fig. 3G,H): Characterised by its large size and usually strongly contrasting markings. Forewing ground colour always pale, ranging from pale bluish or greyish white to pure white; fasciae usually well defined, dark grey to black, orange scaling often absent. Hindwing dark grey-brown to brown.
Female (Fig. 4H): Only one, slightly worn, specimen known, typical *Sphaleroptera* type, whitish ground colour with two dark fasciae. Relatively small compared to the size of the known males.
♂ **genitalia** (Fig. 5J-L; Fig. 6G; Fig. 7F,G): Similar to *S. a. buseri*, but projection at tip of phallus approx. twice as long, directed downward nearer to 90° from the shaft and twisted to right (viewed towards tip), lateral ridge of shaft absent; sacculus bifurcations slightly diverging, of equal length, the dorsal arm sometimes slightly narrower, but both more or less rounded at tip.
♀ **genitalia** (Fig. 8I): Similar to *S. a. buseri*, but ostium bursae not as deep, antrum heavily sclerotized, narrower, strongly bifurcate and divergent, ventrally curved to right at tip, acutely pointed with broad long membranous pouch.

Derivatio Nominis
Named after the area where most specimens have been found.

Life history and biology
The few known specimens with precise data were taken between 10th July and 4th August. The early stages are unknown.

Distribution (Fig. 10)
Known only from the Adamello Alps of northern Italy except for one old specimen from Monte Piano (South Tyrol, Sexten Dolomites). Altitudinal range: 2500–2800m.

Remarks
Due to the remarkably long phallus tip, very large size, contrasting coloration and isolated occurrence in the southern Alps, this taxon is considered to be a good species.
The species most probably originated from a prototype *alpicolana* population that became isolated in this part of the southern Alps after a glaciation event. Interestingly, from the male and female genitalia it appears to be most closely related to *S. a. buseri*, but this seems unlikely considering the current distributions of the two taxa, although it is possible that a *buseri* population also became displaced southeastwards during a glaciation period and reached the Adamello Alps.
The occurrence of this species on Monte Piano is interesting, but requires confirmation, as it is possible that this old specimen has sometime accidentally acquired the wrong label.

***Sphaleroptera orientana* sp.n.**
Euledereria alpicolana sensu OBRAZTSOV 1955, ♂ genitalia Figs 310–313.

Material examined: 46♂,6♀
Holotype: 1♂, 'Austria merid, Osttirol, Schobergr., Alkuser Scharte, 2630m 10.8.1988, leg. Tarmann' 'Holotype' 'S.E.W. GP No. E.524 ♂ ' [TLMF] – **Paratypes: Austria:** 2♀, Austria merid., Osttirol, Virgental, Venedigergruppe, Umg. Eissee, 2600–2800m, 12.8.1993, leg. Ryrholm [TLMF]; 1♀, Austria merid., Osttirol, Virgental, Venedigergruppe, Sajathütte E, 2450–2550m, 10.8.1993, leg. Ryrholm [TLMF]; 5♂, Austria merid., Osttirol, Virgental, Venedigergruppe, Umg. Eissee, 2600–2800m, 12.8.1993, leg. Ryrholm [TLMF]; 1♂, Austria merid., Osttirol, Virgental, Venedigergruppe, Umg. Eissee, 2600–2800m, 12.8.1993, leg. Ryrholm [TLMF] GP E.604; 5♂, Austria, Gr.Venediger, viii.51, leg. Pinker [TLMF]; 1♂, Austria merid, Osttirol 2700–2750m, Granatspitzgruppe, S Nüssing Scharte E., 15.8.1991, leg. Tarmann [TLMF]; 1♂, Austria merid, Osttirol 2960–3030m, Granatspitzgruppe, Wallach Köpfe, 15.8.1991, leg. Tarmann [TLMF]; 1♂, Austria merid, Osttirol 3192m, Granatspitzgruppe, Kl. Muntnitz, 15.8.1991, leg. Tarmann [TLMF]; 1♂, Austria, Osttirol, Glocknergruppe above Kals, 1700–2200 m, 29.vii.1991, Karsholt & Rakosy, [ZMUC]; 1♂, Austria merid, Osttirol 2500m, Schobergruppe, Anthofhütte NW, LF31 Nasensteig 1.9.1991, leg. Tarmann [TLMF]; 1♂, Austria merid, Osttirol 2480–2530m, Schobergruppe, Anthofhütte NW, Nasensteig 2.9.1991, leg. Tarmann [TLMF]; 2♂, Austria merid, Osttirol 2400m, Schobergruppe, Hochschober Hütte S. Nase, 1.9.1991, leg. Tarmann [TLMF]; 4♂, 1♀, Austria merid, Osttirol 2680–2720m, Schobergruppe, Mischach Scharte, 2.9.1991, leg. Tarmann [TLMF]; 5♂, Austria merid, Osttirol 2760–2880m, Schobergruppe, Bawenek Scharte E., 29.8.1991, leg. Tarmann [TLMF]; 1♂, Austria merid, Osttirol, Schobergr., Alkuser Scharte, 2630m 10.8.1988, leg. Tarmann [TLMF] GP E.523; 2♂, Austria merid, Osttirol, Schobergr., Alkuser Scharte, 2630m 10.8.1988, leg. Tarmann [TLMF]; 5♂, Austria merid, Osttirol, Schobergr., Alkuser Scharte, 2630m 8.8.1988, leg. Tarmann [TLMF]; 1♀, Austria merid, Osttirol, Schobergr., Alkuser Scharte, 2630m 8.8.1988 / leg. Tarmann [TLMF] GP E.527; 1♀, Schober-Gr., 2200m, 28.vii.1923, Coll.R.Kitschelt [NHMW] GP E.529; 1♂, Carinthia, Gross Glockner, f. 23.vii.93, Coll. Krone [MTMB] GP E.471; 1♂, Carinthia, Gross Glockner, f. 24.vii.93, Coll. Krone [MTMB]; 1♂, Pasterze, Juli 05 [NHMW]; 1♂, 31/7/10, Styria, Höchstein, Lorbruk [?], 2200m [NHMW]; 1♂, Austria sup., Speikwiese, 8.viii.1920, 2000m, leg. Knitschke [NHMW]; 1♂, Austria superior, Gr. Pyrghas, 1800m, 3.8.1941, leg. J.Klimesch [Coll.Klimesch]; 1♂, Austria superior, Warscheneck, 2000m, 30.vii.1923, leg. J.Klimesch [Coll.Klimesch]; 1♂, Warscheneck, Ob-Öst., 7.8.[19]02 [NHMW] GP E.530 – **Italy:** 1♂, Alpi Carniche, Sappada 9.8.935, L.O-Olbe m.2000, G. Della Beffa [MCSN].
Other material: Switzerland: 1♂, 600, 63, Suisse, Staudinger, Coll. Blachier [MHNG] GP E.611 – **Austria:** 1♂, [no label, coll. Staudinger, ZMHB].

Description and diagnosis:

Wingspan: males 15.5–19.5 mm; median 17.5 mm, n=39; females 13.0–15.0 mm; median 13.8 mm, n=4
Characterised by rather indistinct markings, subbasal fasciae usually better defined than medial fascia.
Male (Fig. 3I,J): Legs grey, sprinkled white, tarsi weakly ringed white, spurs grey above, white below; head, frons, palpi and antenna dark grey, only weakly sprinkled white; white patch of scales below palpi; Forewing ground colour pale grey or brown, many narrowly tipped white, overlaid with white or bluish scales, black markings usually overlaid with orange-brown scales, except along costa; fringe grey or brown, often mixed whitish, post terminal line usually not well defined; some specimens from Upper Austria extensively overlaid with pale whitish-grey scales. Hindwing grey or brown.
Female (Fig. 4I,J): Typical *Sphaleroptera* type, whitish ground colour with two dark fasciae.
♂ **genitalia** (Fig. 5M-O; Fig. 6H; Fig. 7H,I): Similar to *S. a. alpicolana*, but left-hand wall of phallus tapering slightly at tip, projection very thin and poorly sclerotized, sometimes absent, but often reaching ventral edge of the shaft; a characteristic short tooth-like process at tip laterally on left side (viewed towards tip) projecting at right angles; occasionally some tiny serrations along shaft dorsally. The two arms of the sacculus bifurcation approximately of equal length, more or less parallel and as broad across as the length of the arms. The dorsal arm usually pointed, the ventral arm blunt, often squarish at tip.
♀ **genitalia** (Fig. 8J,K): Antrum heavily sclerotized, narrowed at middle, not bifurcate, but weakly bilobed, right-hand lobe (viewed ventrally) extends into the short straight ductus bursae, left-hand lobe blind. The latter corresponds to the right hand or most ventral lobe of the previously described species. The antrum in *orientana* is therefore twisted to the left by 90° compared to that in *S. a. alpicolana*. The start of the ductus seminalis is therefore more visible in preparations, emanating from the right-hand side of and at the beginning of the ductus bursae.

Derivatio Nominis

From the Latin '*oriens*' = east, referring to the eastern Alpine distribution of the species

Life history and biology

Adults have been found between 23rd July and 2nd September. The early stages of this species are not known.

Distribution (Fig. 10)

Through the central Austrian Alps (Upper Austria, Styria, Carinthia, East Tyrol, just reaching into northern Italy (Carniche Alps). Altitudinal range: 1800–3192m.
The distribution overlaps with that of *S. dentana*. A specimen labelled 'Suisse, Staudinger' is present in the Geneva Natural History Museum, but based on our current knowledge of the distribution, this specimen has most likely been mislabelled. Herbert (1961) reports '*alpicolana*' from additional localities in central and eastern Austria, which most likely refer to this species: Preber, Sulzenhals near Filzmoos, Taferlscharte (all in Salzburg) and Raxalpe (Lower Austria).

Remarks

Especially the female genitalia show this taxa to be a separate species, although it is clearly closely related to the previously treated *Sphaleroptera* species. *S. orientana* has been found flying together with *S. dentana* at several localities in East Tyrol (same day, same locality), thereby demonstrating that these two taxa are genetically completely separate.

***Sphaleroptera orientana suborientana* ssp.n.**

Material examined: 11♂

Holotype: 1♂, 'Italia sept., Südtirol, 2050m, Sella-Gruppe, SO Grödnerjoch, 11.8.1991, leg. Huemer' 'Holotype' 'S.E.W. GP No. E.614 ♂ ' [TLMF] – **Paratypes: Italy:** 1♂, Norditalien, Rosengarten, A.9.71 2100m Fr.Zürnbauer Mü. [TLMF]; 1♂, Norditalien, Rosengarten, A.9.71 2100m Fr.Zürnbauer Mü.

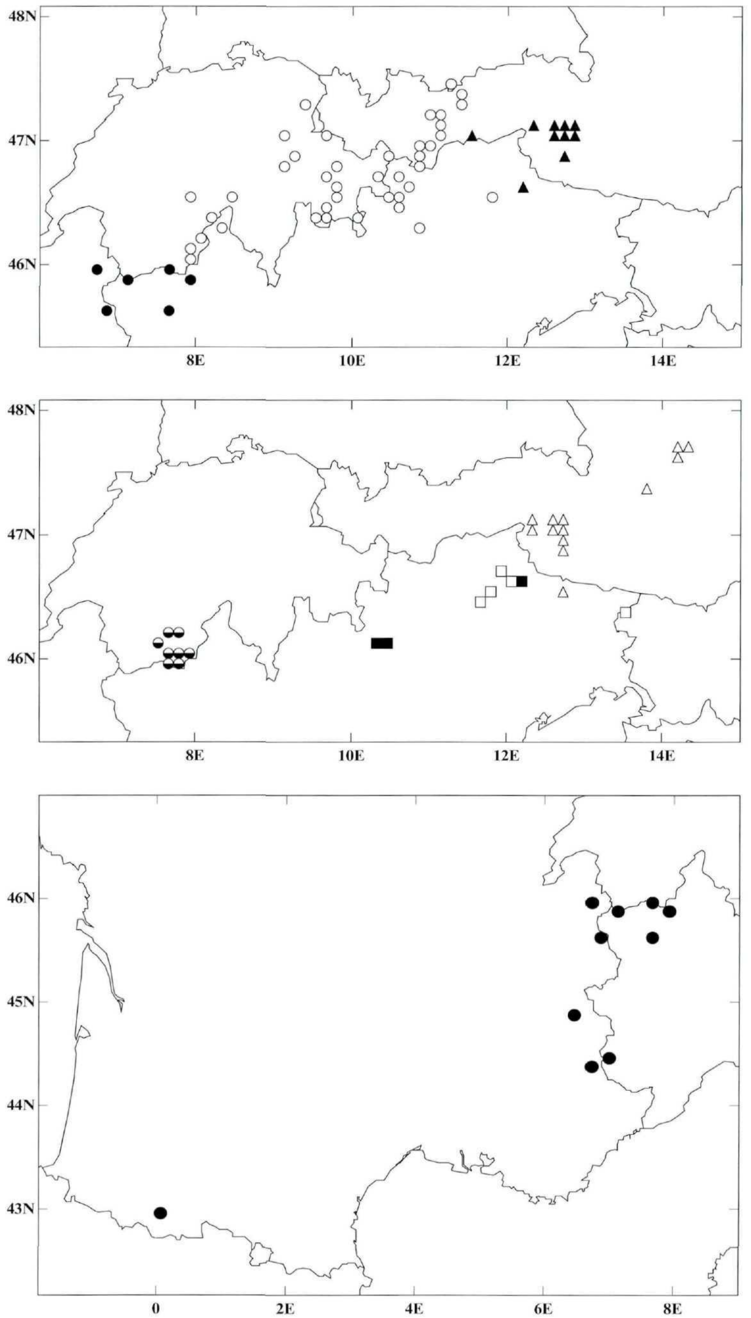

Fig. 10: Distribution maps of *Sphaleroptera* species: Top and middle, centred on Switzerland, Austria and northern Italy – *S. a. alpicolana* (open circles), *S. dentana* (filled triangles) and *S. occidentana* (part only, filled circles), *S. a. buseri* (filled/open circles), *S. adamelloi* (filled squares), *S. o. orientana* (open triangles), *S. o. suborientana* (open squares); Bottom, centred on southern France – *S. occidentana* (filled circles).

[TLMF] GP E.503; 4♂, Italia sept., Südtirol, 2050m, Sella-Gruppe, SO Grödnerjoch, 11.8.1991, leg. Huemer [TLMF]; 1♂, Venezia Tridentina, Val di Marebbe, Fanes Pico m. 2100 / 10.vii.931, L. Rocca legit, Coll. Della Beffa [MCSN] GP E.476; 2♂, Venezia Tridentina, Val di Marebbe, L. Colli Alti m. 2250 / 31.vii.931, L. Rocca legit, Coll. Della Beffa [MCSN]; 1♂, Italia sept., Prov. Udine, Alpi Giulie, Rif. Gilberti 2050 3.8.1987, leg. Huemer [TLMF] GP E.504.

Description and diagnosis:

Wingspan: males 17.0–19.0 mm; median 18.0 mm, n=11

A relatively large, rather uniformly grey, weakly marked taxon, somewhat reminiscent of *Eana incanana* STEPHENS (1852).

Male (Fig. 3K,L): Antennae more clearly ringed white than in *S. o. orientana*. Hind legs very pale grey, with many long whitish scales. Forewing pale brownish or bluish grey with black spotting reduced to form thin cross-lines, fasciae only slightly darker grey, often not reaching dorsum, some darker scales tipped white, post terminal line dark, tipped white. Specimen from Rif Gilberti heavily sprinkled white, similar to *ademelloi*, but with paler brown/grey fascia. Underside very pale grey, 9 white costal spots, dorsum white. Hindwing grey or brown.

Female: Unknown.

♂ **genitalia** (Fig. 4P-R; Fig. 5I; Fig. 6J,K): Differs from *S. o. orientana* by a significantly more sclerotized and usually longer projection at the tip of the phallus, but much shorter than in *S. a. alpicolana*. Phallus slightly longer than nominate subspecies: *S. o. orientana* range: 0.925 – 1.025 mm (n=6); *S. o. suborientana* range: 1.10 – 1.15 mm (n=4).

♀ **genitalia**: Not known.

Life history and biology

The few known specimens were taken between 10th July and 11th August. The early stages of this species are not known.

Distribution (Fig. 10)

Northern Italy: Dolomites. A solitary specimen from the Julian Alps on the border to Slovenia probably also belongs to this subspecies. Altitudinal range: 2050–2250m.

Remarks

The differences in the tip of the phallus between this subspecies and the nominate subspecies, coupled with the more southerly distribution and, at least in the west, the uniformly grey coloration, are considered to be sufficient to warrant subspecies status.

***Sphaleroptera dentana* sp.n.**

Material examined: 43♂,13♀

Holotype: 1♂, 'Austria merid, Osttirol 2400m, Schobergruppe, Hochschober Hütte S. Nase, 1.9.1991, leg. Tarmann' 'Holotype' [TLMF] – **Paratypes: Austria:** 1♂, Austria occ. Teriolis sept., Zillertaler Alpen, SW Landshuter Hütte, 2630m 21.7.1988, leg. Tarmann [TLMF]; 1♂, Tirol, Vennspitz, 3.8.38 2300m, R. Scholz [USMC]; 4♂, Austria, Gr.Venediger, viii.51, leg. Pinker [TLMF]; 1♂, Austria merid, Osttirol 2960–3030m, Granatspitzgruppe, Wallach Köpfe, 15.8.1991, leg. Tarmann, [TLMF]; 13♂, 1♀, Austria, N Tirol, Glocknergruppe above Kals, 1700–2200 m, 29.vii.1991, Karsholt & Rakosy [ZMUC]; 1♀, Glockn., Mann [NHMW] GP E.531; 1♂, Glockner, Krone [NHMW] GP E.528; 1♂, Glockn. 1886, Coll. Lederer [coll. Staudinger, ZMHB]; 3♂, Austria merid., Osttirol, 2300m Glocknergruppe, Golemizil, 11–12.7.1988, leg. Tarmann [TLMF]; 1♂, 1♀, Austria merid, Osttirol 2760–2880m, Schobergruppe, Bawenek Scharte E., 29.8.1991, leg. Tarmann, [TLMF]; 1♀, Austria merid, Osttirol 2760–2880m, Schobergruppe, Bawenek Scharte E., 29.8.1991, leg. Tarmann [TLMF] GP E.613; 1♂, Schober-Gr., 2300m, 29.vii.1923 [Coll.R.Kitschelt, NHMW]; 1♂, Carinthia 1880[?] [coll. Staudinger, ZMHB]; 1♂, Carinthia, Hl.Blut, Schareck, 10.8.1969, 2300m, leg. J.Klimesch [Coll. Klimesch]; 1♂, Pasterze, 1870 [NHMW]; 1♂, Steyerm. 1857 [NHMW]; 1♂, Steyerm., 1856 [NHMW]; 1♂, Styr., M[an]n [NHMW]; 1♂, Sphaleroptera alpicolana, Styrie, [coll. L. Paravicini, NHMB] GP E.441 – **Italy:** 1♂, Mont Piano 1876 [reverse side of label: Mann 1876, Schludebach] [NHMW] GP E.605; 1♀, Mont Piano 1876 [reverse side of label: Mann 1876, Schludebach] [NHMW] GP E.525.

Other material: Austria: 11♂, 23♀ (11♂, 2♀ gen.det.), Glockner Hochtor 2500m, XII 11.9. – 1.11.78 [TLMF, preserved in alcohol]; 1♂, [no label, ETHZ], GP E.473 (ETH1288); 5♂, [no label, ETHZ]; *Females probably belonging to this species (genitalia not checked)*: 1♀, Coll. Led[erer] [coll. Staudinger, ZMHB]; 1♀, Glockn. 1886 / Coll. Led[erer] [coll. Staudinger, ZMHB]; 1♀, Led[erer]Glok., 1861 [NHMW]; 1♀, Glockn., Mann [NHMW]; 1♀, Carinthia, Glockner, Zerny, 3.8.21 [NHMW]; 1♀, Carinthia, Glockner, Zerny, 3.8.21 [NHMW]; 1♀, Pasterze, 1861 [NHMW].

Description and diagnosis:

Wingspan: males 14.5–19.5mm, median 16.0 mm, n=42; females 12.0–13.2 mm, median 12.5 mm, n=10 A generally small, rather dark species often with two roundish medial spots at one third and one half. On average both male and female smaller than the sympatric *S. orientana*.

Male (Fig. 3M,N): Antennae dark grey, not or weakly ringed white. Forewing ground colour ranging from brown to whitish-grey; dark brown subbasal and medial fasciae often not reaching dorsum and reduced or absent towards costa, the centre part of the fasciae often forming two large roundish spots; often three to six whitish costal spots present. Orange-brown scaling sometimes present. Hindwing brown.

Female (Fig. 4K,L): Markings basically similar to male, the two roundish spots often prominent, ground colour often brown, but as with other species can be much paler, with strong orange scaling.

♂ genitalia (Fig. 5S,T; Fig. 6J; Fig. 7L): Similar to *S. alpicolana*, but phallus very different, shaft rather shorter and thicker, tip extended ventrally and curved 90° to right (viewed towards tip), a short tooth-like process laterally at tip, similar to that in *S. orientana*, right-hand side of shaft wall at tip developed into a large flat tooth-shaped projection, leaning outwards; arms of sacculus bifurcation relatively long, tips rounded or square.

♀ genitalia (Fig. 8L-N): Ostium bursae broader than *S. orientana*, antrum heavily sclerotized, shorter and broader than any other species of the genus (twice as long as broad), more or less skewed to left (viewed ventrally), widening towards equally wide ductus bursae; lamella antevaginalis short, reaching about only half way down antrum.

Derivatio Nominis

From the Latin '*dens*' = tooth, referring to the tooth-like projections at the tip of the phallus.

Life history and biology

Adults have been found between 11th July and 1st September. The early stages of this species are not known.

Distribution (Fig. 10)

Austria: Stretches from Styria (precise localities not known), Carinthia and East Tyrol to the Zillertal Alps of North Tyrol (Vennspitze); two specimens also know from northern Italy (Monte Piano, Sexten Dolomites). Altitudinal range: 2,200–2,960 m.

Flies sympatrically with *S. orientana* over much of its range. Six unlabelled specimens are present in the general Swiss collection of the ETH in Zurich. Furthermore, Josef Razowski sent the author a drawing of the male genitalia of a *dentana* specimen labelled "Tessin, Schweiz". It is therefore possible that a population of this species could yet be found in Switzerland, but no recent or confirmed material exists.

Remarks

Morphologically a very distinct species, clearly genetically isolated from the sympatric *S. orientana*, although, based on the female genitalia, is closer to that species than to the other species of the *S. alpicolana* group.

Discussion

One intriguing question with such a high Alpine brachypterous genus is how it managed to extend its range over much of the Alps and the Pyrenees, and how speciation occurred. Clearly the Pleistocene glaciations played a very important role in both of these aspects and this subject was touched upon when discussing *S. a. buseri* and *S. occidentana*.

There does not seem to be many ways for *Sphaleroptera* populations to expand their range. Most obviously, females could follow slowly shifting habitats. Larvae or eggs could be carried down into valley bottoms by rock slides and if sufficient foodplant was available, emerging females could ascend the other side of the valley. It is also possible that neonate larvae are carried away by the wind before they get a foothold on the larval substrate. Populations would be able to move along exposed ridges, but females would presumably not actively cross permanent snowfields or glaciers. Warm interglacial periods may therefore have helped populations to expand if the extent of permanent snowfields was greatly reduced.

There has been much debate on the rate of speciation among insects. Evidence from quaternary fossils, mainly of Coleoptera, point to both species constancy, despite isolation, over millions of years, and high divergence rates (e.g. in Nearctic montane areas) within the last 10,000 years (ELIAS 1993). More recently, molecular studies, especially of mitochondrial DNA, have also demonstrated large ranges in speciation rates among various animal groups (HEWITT 1996; HEWITT 1999; HEWITT 2000). Divergency was probably favoured in high Alpine species during the Quarternary, due to the continually changing environmental pressures. It seems therefore quite feasible that speciation could have occurred among *Sphaleroptera* within the 0.5–1 myr period and subspeciation well within 0.5 myr, although *S. dentana* probably diverged well before this period.

Another example of a high altitude brachypterous genus of Lepidoptera is *Sattleria* POVOLNÝ... 1965 (Gelechiidae), which shares similar habitats, behaviour and foodplants with *Sphaleroptera*, although the adults are nocturnally active (PITKIN & SATTLER 1991; HUEMER & SATTLER 1992). It also occurs in the Pyrenees, but its range extends further east in the Alps and also occurs in the Apennines, Carpathians and Balkans. Three species of *Sattleria* are known from the Pyrenees, but unlike *S. occidentana*, none of these are thought to also occur in the Alps. *Sattleria* may therefore have reached the Pyrenees earlier than *Sphaleroptera*, giving more time for speciation to occur, although it is also possible that other *Sphaleroptera* species will be found. *Sattleria* might have expanded its range eastwards at the same time, thereby giving an explanation as to why *Sattleria* is more widely distributed than *Sphaleroptera*. This would support the hypothesis that speciation within such high Alpine brachypterous Lepidoptera could have occurred within the 0.5–1 myr period.

It is suggested that *S. a. buseri* survived the Pleistocene glaciations on nunataks in southern Valais. Several other insect species are thought to have similarly survived this period (BESUCHET 1968). However, for *Sphaleroptera* to have survived, a larval foodplant must also have occurred on these nunataks. Several molecular studies have been undertaken recently to answer the question as to whether certain Alpine plant species could have survived "*in situ*" during the last ice age on exposed mountain peaks above 3,000m (the nunatak hypothesis) or whether all life in the glaciated areas was eradicated, their survival depending on available peripheral refugia (the "*tabula rasa*" hypothesis) (STEHLIK 2003). The only known larval foodplant of *S. a. buseri*, *Saxifraga oppositifolia* is one of those plants studied (HOLDEREGGER et al. 2002). However, little evidence could be found that this widespread species survived on nunataks during the ice age, but neither could the hypothesis be disproven. The genotypes of immigrants from peripheral refugia are thought to have swamped out any possible genotypes of nunatak populations. On the other hand, a probable nunatak survival could be demonstrated in the case of another high alpine cushion plant, *Eritrichium nanum* (King of the Alps, Boraginaceae), by an analysis of chloroplast DNA (Stehlik et al. 2002). Strong hotspots of high genetic diversity, indicating nunatak survival, were found between populations in southern Valais (Gornergrat, Saas Fee and Augstbordpass), but also in Styria and Carinthia in Austria (Hafner, Hochgolling and Eisenhut). These populations were also the most divergent from the most common, and evolutionarily ancestral, haplotype, which was found in most other populations from Simplon to the Ortler group, but also along the southern edge of the Alps to Slovenia. The hotspot of nunatak survival in the eastern central Alps was confirmed by another study looking at *Saponaria pumila* (Dwarf Soapwort, Caryophyllaceae) (Tribsch et al 2002).

These findings fit with the hypothesis that certain *S. a. buseri* populations could also have survived the Pleistocene ice ages on nunataks, feeding on either *Eritrichium* itself or another nunatak survivor, probably including *Saxifraga oppositifolia* and *Silene acaulis*. *S. occidentana* and *S. a. alpicolana* on the other hand most likely retreated to peripheral refugia in the south-west and north-east or/and south-east respectively, although nunatak survivals of *S. occidentana* on the highest peaks of the south-western Alps and *S. a. alpicolana* in the central Alps, e.g. in Grisons, cannot be excluded. It is possible that *buseri* and *alpicolana* populations repeatedly came close during each interglacial period, allowing a minimal gene flow to occur.

In the east, a few specimens of *S. orientana* are known from the area identified by Stehlik (et al. 2002) as a nunatak survival area of *Eritrichium*. It is therefore possible that populations of this species remained *in situ*, perhaps allowing *S. o. suborientana* to evolve.

Several *Sphaleroptera* taxa are characterised by a more or less long projection at the tip of the phallus. In those same taxa, the female possesses a membranous pouch below the antrum, which most likely accomodates the male phallus projection during mating. A male with a shorter projection could probably physically mate with females of taxa with a longer pouch, assuming any necessary pre-mating stimuli are still functioning. This could explain the apparently successful mating between a male *S. a. alpicolana* and female *S. a. buseri* observed in captivity. A mating between a male *S. adamelloi* with any other *Sphaleroptera* female on the other hand would seem to be physically impossible, whereas a female *S. adamelloi* could probably mate with any other *Sphaleroptera* taxa male. A male *S. a. buseri* would probably have difficulty in mating with either of its neighbouring taxa, i.e. *S. a. alpicolana* and *S. occidentana*. However, both of the latter taxa could probably mate with a female *S. a. buseri*, so if any gene flow exists between these taxa it could only be towards *buseri*, not in the other direction. It would appear that a mating between *S. a. alpicolana* and *S. occidentana* is not possible in either direction. The *S. dentana* antrum is wide enough for the male phallus tip to pass down, the curved apical process probably fitting in the rounded opening of the ductus bursae. A male *S. dentana* probably could not mate with any other *Sphaleroptera* female.

A molecular genetic study of the *Sphaleroptera* complex would help to clarify the phylogenetic relationships between the various taxa and possibly also give some insight into their movements and speciation during the late pleistocene.

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