

High altitude Tipulidae in Switzerland (Diptera, Nematocera)

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Abstract. An overview is given of 21 species of the alpine and subalpine Tipulidae fauna. Thermic levels based on plant phenology are used to classify the species. The sequence obtained is followed to discuss systematics, morphological adaptations (melanism, brachypterism, dense body clothing, small size), habitat selection (coniferous forest, shrub zone, alpine meadow, streams or other wet biotopes, bedrock or loose rock-screes, moraine, avalanche) and biogeography (distribution patterns including boreo-alpine). Alpine species are mostly alpine endemics, rarely distributed in other Central European mountains, missing in Scandinavia or represented there by subspecies or morphologically distinct populations. Many subalpine species show on the contrary large distributions including boreo-alpine and three are represented by subspecies in Southern Europe. A Siberian origin of some subalpine and upper montane species is discussed.

Key words: Tipulidae, *Tipula crolina* nom. nov., alpine, Swiss Alps, brachypterism, endemic.

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INTRODUCTION

Publications dealing with the Tipulids of the alpine region are still very scarce. Apart from taxonomical works (mainly MANNHEIMS & THEOWALD in LINDNER (1953-1980) we can only mention the faunistical lists of MANNHEIMS & PECHLANER (1963) for North Tirol; THEISCHINGER (1977) for Allgäu and THEISCHINGER (1978) for Oberösterreich. Lists of boreo-alpine tipulids have been proposed by MANNHEIMS (1959) and recently THEOWALD & OOSTERBROEK (1985) have discussed in detail the zoogeography of montane, alpine and boreal Tipulidae. The *excisa*-group of *Vestiplex* has been revised by THEOWALD & MANNHEIMS (1962).

In Switzerland the alpine fauna has only rapidly been described within the general inventory of the fauna (DUFOUR 1986).

The present publication is aimed to give an overview of the various remarkable features of the alpine and subalpine fauna, including systematics, morphology, ecology and biogeography. Only Swiss material has been taken into account in order to work on strictly

comparable data which can be linked to ecological informations. Very few alpine species are not represented in Switzerland and consequently our conclusions concern the whole alpine system.

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METHODS

The Swiss fauna has been studied over more than 10 years. As a result a large database is now available which describes the captures of 41235 specimens representing 9551 occurrences of 151 (sub)species. Among the various ecological informations the most appropriate to describe high altitude insects appears to be the thermic levels based on plant phenology as proposed by SCHREIBER 1977. Altitude is a less reliable parameter as vegetation levels may vary considerably even within the small Swiss territory. For instance the subalpine-alpine limit is found at elevations of 1500-1700 m in the Jura while it can be as high as 1900-2400 m in the central Alps (HESS, LANDOLT & HIRZEL 1967).

The limits of the vegetation levels may be easily correlated with the thermic levels (TH) of SCHREIBER numbered in DUFOUR 1986 as follows:

TH <3	: alpine
3 ≤ TH < 6	: subalpine
6 ≤ TH < 11	: montane
11 ≤ TH	: colline

Furthermore, the thermic levels can be correlated with the duration of vegetation growth, average temperature of months April-October, and yearly average temperature as given for the alpine and subalpine levels in Tab. I.

Within the database, abundance classes were preferred to sums of individuals or numbers of occurrences. Being semi-quantitative, abundance classes have the advantage of reducing importance of massif catches, without neglecting totally high densities of individuals.

Table I
Climatical conditions at alpine and subalpine vegetation levels

TH	Climatical conditions*	Level
1	55 days/<3.5°C/<0°C	alpine
2	55-80 days/3.5-5.0°C/± 0-1.0°C	- " -
3	80-100 days/5.0-6.0°C/1.0-2.0°C	subalpine
4	100-120 days/6.0-7.0°C/2.0-3.0°C	- " -
5	120-135 days/7.0-8.0°C/3.0-4.0°C	- " -

*Climatical conditions: duration of vegetation growth/average temperature of months April-October/yearly average temperature.

The abundance classes are defined here exponentially:

N. individuals:	1	2-4	5-8	9-16	17-32	etc.
Ab. classes:	I	II	III	IV	V	

RESULTS

List of alpine and subalpine Tipulidae

For each of the 151 (sub)species of the Swiss fauna, average thermic level (TH) was computed on the base of abundance classes for specimens caught only by non attractive collecting techniques (sweep-net, Malaise trap, Barber pitfall, yellow plates and emergence traps).

Table II gives the list of species ordered by decreasing average thermic level (AvgTH): 8 species appear as being alpine ($\text{AvgTH} < 3$) and 12 subalpine ($3 \leq \text{AvgTH} < 6$). Both groups are well separated as no species is found with AvgTH between 2.8 and 3.7. Below are listed for information 18 upper montane species ($6 \leq \text{AvgTH} < 8$) which will not be analysed here.

This method is not only efficient to detect alpine and subalpine Tipulidae, but it locates clearly each species within its vegetation level, and helps greatly to define ecological needs. Furthermore the sequence of species will be used in further discussion of systematical, morphological, ecological and biogeographical features.

One must remark that three species are very poorly represented and that their position in the sequence remains uncertain: *T. sauteri* was only caught once by hand (1♂, 1♀, Gornergrat, Rotenboden, 2800 m) and *T. luridorostris* only rarely taken by hand, although it is less uncommon in nocturnal catches, at slightly lower elevations. Secondly, *T. bilobata* POKORNY, 1887 was only collected once in Switzerland at night at subalpine level. Data from literature concerning this species refer mostly to high altitude captures: up to 2630 m in North Tirol (MANNHEIMS & PECHLANER 1963), but also exceptionally 600 m! in the Karawanken (THEOWALD 1980). Known to live in rocky limestone habitats, *bilobata* is most likely to be an alpine species and we shall consider it as such below.

In a similar way we have computed for comparison species average altitude (Avgalt), ordered by decreasing avgalt (Table III) for diurnal captures. This table shows only slight differences with Table II in sequences of species (see *T. gimmerthali*, *T. circumdata*), but is less convincing when confronted to field observations. However, Table III gives interesting information on maximal altitude of captures, such of those of *T. glacialis* at 3100 m, near Zermatt (Gornergrat) where copula was observed in well exposed screes. This is to our knowledge the highest mention of reproduction of Tipulidae in the Alps.

Systematical, morphological and ecological features

The groups of alpine and subalpine Tipulids being defined, their systematical, morphological and ecological features may be discussed (Table IV).

Table II

Alpine, subalpine and upper montane Tipulidae (in relation with thermic levels)

SPECIES	SUM classes	MIN TH	MAX TH	AVG TH	stddev	VEGETATION LEVEL
<i>Tipula sauteri</i> DUFOUR, 1982	2	1	1	1.0	0.0	Alpine
<i>Tipula crolina</i> nom. nov.	63	1	6	1.5	0.9	
<i>Tipula glacialis</i> POKORNY, 1887	37	1	6	1.6	1.2	
<i>Tipula irregularis</i> POKORNY, 1887	28	1	4	2.0	0.9	
<i>Tipula montana</i> CURTIS, 1834	49	1	8	2.4	1.7	
<i>Tipula excisa</i> SCHUMMEL, 1833	151	1	13	2.5	1.6	
<i>Tipula goriziensis</i> STOBL, 1893	21	2	6	2.6	1.2	
<i>Tipula subglacialis</i> THEOWALD, 1980	18	1	6	2.7	2.1	
<i>Tipula h. strobliana</i> MANNHEIMS, 1966	60	1	9	3.8	1.6	Subalpine
<i>Tipula luridorostris</i> SCHUMMEL, 1833	4	3	5	4.0	1.2	
<i>Tipula cisalpina</i> RIEDEL, 1913	27	1	9	4.3	1.7	
<i>Tipula mayerduerii</i> EGGER, 1863	9	3	6	4.3	1.6	
<i>Tipula pallidicosta</i> PIERRE, 1924	26	2	8	4.4	1.6	
<i>Tipula pseudopruinosa</i> STROBL, 1895	8	2	7	4.5	2.4	
<i>Tipula austriaca</i> POKORNY, 1887	8	2	9	4.6	2.5	
<i>Tipula subnodicornis</i> ZETT., 1838	98	1	8	4.7	1.8	
<i>Tipula alpium</i> BERGROTH, 1888	33	1	13	4.8	3.6	
<i>Tipula grisescens</i> ZETTERSTEDT, 1851	11	2	8	4.8	2.6	
<i>Tipula gimmerthali</i> LACKSCHEWITZ, 1925	89	2	9	5.5	1.4	
<i>Tipula i. subinvenusta</i> SLIPKA, 1950	21	2	9	5.6	2.2	
<i>Tipula tulipa</i> DUFOUR, 1983	1	6	6	6.0	0.0	Upper Montane
<i>Tipula limbata</i> ZETTERSTEDT, 1838	53	3	9	6.1	1.5	
<i>Tipula circumdata</i> SIEBKE, 1863	13	4	7	6.1	1.1	
<i>Tipula melanoceros</i> SCHUMMEL, 1833	40	5	7	6.1	0.6	
<i>Tipula mikiana</i> BERGROTH, 1888	19	2	16	6.2	3.3	
<i>Prionocera turcica</i> (FABRICIUS, 1781)	43	6	7	6.2	0.4	
<i>Tipula pseudoirrorata</i> GOETGHEGUER, 1921	5	5	8	6.2	1.3	
<i>Tipula neurotica</i> MANNHEIMS, 1966	80	2	15	6.5	2.9	
<i>Tipula limitata</i> SCHUMMEL, 1833	28	3	12	6.6	2.3	
<i>Tipula subvafra</i> LACKSCHEWITZ, 1936	30	5	9	6.7	1.1	
<i>Tipula pagana</i> MEIGEN, 1818	37	5	13	6.9	2.1	
<i>Tipula subsignata</i> LACKSCHEWITZ, 1933	74	2	15	7.0	2.7	
<i>Prionocera pubescens</i> LOEW, 1844	9	6	9	7.2	1.1	
<i>Tipula zernyi</i> MANNHEIMS, 1952	28	2	14	7.6	2.8	
<i>Dolichopeza albipes</i> (STROM, 1768)	9	7	9	7.7	0.9	
<i>Tipula fasciculata</i> MANNHEIMS, 1966	3	7	9	7.7	1.2	
<i>Tipula saginata</i> BERGROTH, 1891	4	6	9	7.8	1.3	
<i>Tipula serrulifera</i> ALEXANDER, 1942	10	5	13	7.8	2.7	

Table III

Alpine and subalpine Tipulidae (in relation with altitude)

SPECIES	SUM classes	MIN alt	MAX alt	AVG alt	stddev	VEGETATION LEVEL
<i>Tipula sauteri</i>	2	2840	2840	2840		Alpine
<i>Tipula glacialis</i>	37	1608	3100	2452	357	
<i>Tipula crolina</i>	63	1600	2876	2417	201	
<i>Tipula montana</i>	49	1100	3100	2322	416	
<i>Tipula irregularis</i>	28	1700	2725	2280	281	
<i>Tipula excisa</i>	151	616	2840	2211	323	
<i>Tipula goriziensis</i>	21	1608	2600	2183	273	
<i>Tipula subglacialis</i>	18	1773	2500	2159	264	
<i>Tipula strobliana</i>	60	1060	2500	1953	254	Subalpine
<i>Tipula cisalpina</i>	27	1250	2400	1953	247	
<i>Tipula luridorostris</i>	4	1775	2230	1920	215	
<i>Tipula mayerduerii</i>	9	1580	2149	1855	257	
<i>Tipula austriaca</i>	8	1100	2300	1853	435	
<i>Tipula pallidicosta</i>	26	1400	2250	1773	267	
<i>Tipula alpium</i>	33	634	2500	1758	542	
<i>Tipula grisescens</i>	11	1000	2250	1727	507	
<i>Tipula subnodicornis</i>	98	900	2600	1708	456	
<i>Tipula pseudopruinosa</i>	8	1250	2000	1647	351	
<i>Tipula circumdata</i>	13	1466	1950	1629	177	
<i>Tipula invenusta subinvenusta</i>	21	1220	2250	1588	350	

Systematical, morphological and ecological features

The groups of alpine and subalpine Tipulids being defined, their systematical, morphological and ecological features may be discussed (Table IV).

Systematics: All true alpine or subalpine Tipulids belong to the subfamily Tipulinae (no Dolichopezinae or Ctenophorinae) and to genus *Tipula* (*Nigrotipula*, *Nephrotoma* and *Prionocera* are totally absent). Only 3 subgenera of *Tipula* are represented: *Pterelachisus*, *Savtshenkia* and *Vestiplex* while *Acutipula*, *Beringotipula*, *Dendrotipula*, *Emodotipula*, *Lindnerina*, *Lunatipula*, *Mediotipula*, *Odonatisca*, *Platytipula*, *Schummelia*, *Tipula*, and *Yamatotipula* are all lacking.

This strong selection is probably the result of the aridity of the alpine climate which enables successful breeding only near water or in mosses (*Savtshenkia*) or in meadows for species having developed deep-boring oviposition (*Vestiplex*) which protects the eggs from the rapid dessication occurring during day time on the strongly heated soil surface. Secondly the rock habitats are most favorable to the high altitude species of *Pterelachisus* (except *T. luridorostris* from the subalpine coniferous forest and shrub zone). Only

Table IV

Morphological, ecological and ethological features of alpine and subalpine Tipulidae

Species of <i>Tipula</i> (subgenus)	Brachypterism (ability to fly)	Colour of abdomen	long pilosity on genae	Streams or wet habitata (Mosses)	Loose rock scree, moraine	Meadows	Shrub zone	Coniferous forest	Deep ovi- posi- tion
<i>T. (Pt.) sauteri</i>	+(+?)	grey	-	-	+	-	-	-	-
<i>T. (Vest.) crolina</i>	+(+)	brown	-	-	-	+	-	-	+
<i>T. (Pt.) glacialis</i>	-(+)	grey	+	-	+	-	-	-	-
<i>T. (Pt.) irregularis</i>	-(+)	grey	+	-	+	+	-	-	-
<i>T. (Vest.) montana</i>	+(+)	brown	-	-	-(+)	+	-	-	+
<i>T. (Vest.) excisa</i>	+(+)	brown	-	+	-	+	-	-	+
<i>T. (Sav.) gorizensis</i>	-(+)	grey	-	+	-	-	-	-	-
<i>T. (Sav.) subglacialis</i>	-(+)	grey	+	-	+	-	-	-	-
<i>T. (Pt.) bilobata</i>	-(+)	grey	-	-	+	-	-	-	-
<i>T. (Vest.) h. strobliana</i>	+(+)	grey	-	-	-	-	+	+	+
<i>T. (Pt.) luridorostris</i>	-(+)	brown	-	-	-	-	+	+	-
<i>T. (Vest.) cisalpina</i>	+++(-)	brown	-	-	-	+	+	-	+
<i>T. (Pt.) mayrduerii</i>	-(+)	grey	+	-	+	-	-	-	-
<i>T. (Vest.) pallidicosta</i>	+(+)	brown	-	-	-	+	+	+	+
<i>T. (Pt.) pseudopruiosa</i>	-(+)	grey	-	+	+	-	-	-	-
<i>T. (Pt.) austriaca</i>	-(+)	grey	+	-	+	-	-	-	-
<i>T. (Sav.) subnodicornis</i>	+(-)	grey	-	+	-	-	-	-	-
<i>T. (Sav.) alpium</i>	-(+)	brown	-	+	-	-	-	+	-
<i>T. (Sav.) griseus</i>	-(+)	grey	-	+	-	-	-	-	-
<i>T. (Sav.) gimmerthali</i>	+, ++, +++,-(+,-)	brown	-	+	-	-	-	-	-
<i>T. (Sav.) i. subinvenusta</i>	-(+)	brown	-	+	-	-	-	+	-

Melanism is not conspicuous, although yellow coloured species (*Nephrotoma*, *Lunatipula*) are obviously not present. Table IV indicates colour of abdomen of the species studied. All are more or less brownish (sometime yellowish) or grey. In spite of the fact that grey species are dominant at the alpine level and only equally represented as brown in the subalpine, we do not interpret this as a sign of high altitude melanism but more probably homochromy as grey species are found either on rocky substrate or near water.

On the contrary all meadow species are brownish and only *T. irregularis* (from the rocky upper alpine meadows or boulders), and *T. h. strobliana* (from the subalpine zone and coniferous forests) are grey.

Brachypterism can be present with variable intensity among female Tipulidae and the same species may show all types of wing between strongly reduced (with flight muscles absent) and normally developed and functional (DUFOUR & BRUNIES 1984). In table IV, intensity of brachypterism is indicated with 4 categories (- wing normal, longer than abdomen; + wing slightly reduced reaching between 3/4 of abdomen and tip of cerci; ++ wing reaching about half of abdomen; +++ wing reaching at most the first quarter of abdomen). Ability to fly is indicated separately as even species with slightly reduced wings may be totally incapable of flying (*T. subnodicornis*). It appears that species unable to fly are only lower subalpine (relict in the case of *cisalpina*), whereas at the alpine level all females can fly, at least in warm conditions and once some of the egg-load has been deposited. (A doubt remains for *T. sauteri*, the only female specimen of which was not given the opportunity to fly away, in spite of active wing beat).

Dense body clothing, the advantage of which could be to prevent dessication is not very conspicuous either in alpine Tipulidae in general. However among the species of *Pterelachisus*, unusually long and dense pilosity of genae is found in 5 species, colonizing high altitudes or well exposed screes. On the contrary *T. pseudopruinosa* which lives in sheltered damp subalpine screen does not show this feature, nor do *T. bilobata* and *T. sauteri* still insufficiently known.

Small size is not correlated with high altitude (the small *Savtshenkia* for instance are mostly lower subalpine) and *T. glacialis* is a large species living over 3000 m. It can be concluded that the features listed by MANI do not represent a general trend among Tipulidae. They may be correct while comparing very closely related species as *T. crolina* nom. nov. and *T. montana*: smaller body size, darker body colour and shorter wings in females are all features of the high alpine *T. crolina* stated in DUFOUR 1984 (*T. crolina* nom. nov. is a replacement name for *T. carolae* DUFOUR 1984, preoccupied by *T. carolae* LEWIS 1973).

Ecological features: The main habitats that can be recognized (Figs 1-6) are coniferous forest, shrub zone, alpine meadow, streams or wet habitats with mosses and rock (Mutterstein) or loose (screes, moraine, avalanche). Table IV indicates species found in each type. As already noted in the systematical remarks, the subgenera are all highly specialized. Within each of them every species is again dominant in a certain habitat. Among *Vestiplex* for instance subalpine meadow and pasture are occupied by *T. pallidicosta*; shrub zone and coniferous forest by *T. h. strobliana*; alpine meadow and wet habitats by *T. excisa*;

rocky alpine meadow or boulders by *T. montana* and high alpine discontinuous meadows by *T. crolina*.

Among *Pterelachisus*, limestone screes hold the richest fauna while only *T. irregularis* is found on cristalline rock and boulders. Moraine can offer good habitats for *T. glacialis* or *T. irregularis* much lower than the main high alpine breeding biotopes. It can also offer good breeding grounds for the first species in cristalline regions which are otherwise unsuitable. *T. sauteri* was found on weathered rock with sparse and dry vegetation. Further description of biotopes may be found in DUFOUR 1986.

Biogeographical analysis (Figs 7-29, Tab. V)

Among the 9 species of the alpine level, 5 are distributed only in the Alps (*T. sauteri*, *T. crolina*, *T. irregularis*, *T. subglacialis*, *T. bilobata*), while 2 are present also in other European mountains excluding Scandinavia (*T. glacialis*, *T. goriziensis*). *T. montana* is found outside of Central Europe, but then represented by distinct subspecies (*T. m. verberneae* MANNHEIMS & THEOWALD 1959 in Scandinavia and *T. m. excisoides* ALEX-

Table V

Distribution of alpine and subalpine Tipulidae

Species of <i>Tipula</i> (subgenus)	Alps	Alps Europe mont. excl. Scand.	Europe incl. Scand. Boreo-alpine	Europe Asia	Distribution of subspecies or strongly isolated populations
<i>T. (Pt.) sauteri</i>	+				
<i>T. (Vest.) crolina</i>	+				
<i>T. (Pt.) glacialis</i>		+			
<i>T. (Pt.) irregularis</i>	+				
<i>T. (Vest.) montana</i>		+			Scandinavia, East Siberia
<i>T. (Vest.) excisa</i>		+	?(BA?)		Carpathians, Scandinavia?
<i>T. (Sav.) goriziensis</i>		+			
<i>T. (Sav.) subglacialis</i>	+				
<i>T. (Pt.) bilobata</i>	+				
<i>T. (Vest.) h. strobliana</i>		+			Pyrenees, Carpathians, Asia?
<i>T. (Pt.) luridorostris</i>				+	
<i>T. (Vest.) cisalpina</i>	+				
<i>T. (Pt.) mayerduerii</i>		+			
<i>T. (Vest.) pallidicosta</i>			+(BA)		
<i>T. (Pt.) pseudopruinosa</i>		+			
<i>T. (Pt.) austriaca</i>		+			
<i>T. (Sav.) subnodicornis</i>			+(BA)		Isolated in Central Asia
<i>T. (Sav.) alpium</i>			+(BA)		
<i>T. (Sav.) grisescens</i>			+(BA)		Isolated in Central Asia
<i>T. (Sav.) gimmerthali</i>			+(BA)		Corsica, Pyrenees
<i>T. (Sav.) i. subinvenusta</i>		+			Scandinavia-Asia, S. Nevada

ANDER 1934 in East Siberia). Only *T. excisa* is mentioned from Scandinavia for typical subspecies, while it is surprisingly represented in the Carpathians by *T. e. carpatica* ERIAN & THEOWALD 1961. However HEMMINGSEN & NIELSEN (1965) have shown that *T. excisa* has on an average shorter wings in Scandinavia than in the Alps, which can be interpreted as a certain degree of speciation.

From these informations one can conclude that alpine Tipulidae are mostly alpine endemics, rarely represented in other Central European mountains, missing in Scandinavia or represented by other subspecies or somewhat morphologically different populations.

Biogeography of subalpine species appears to be quite different. Except *T. cisalpina* with brachypterous females, interpreted by MANNHEIMS & THEOWALD 1962 as a relict which found refuge on the Southern side of the Alps during the last ice age, no other species of the subalpine level is restricted to the Alps. Five species are distributed in the mountains of Central Europe. Only the nominal subspecies is known for the rock species of *Pterelachisus* of the subalpine level (*T. austriaca*, *T. mayerduerii*, *T. pseudopruinosa*). On the contrary *T. h. strobliana* is known to be replaced by three subspecies: *T. h. pyrenaei* THEOWALD 1968 in Pyrenees, *T. h. hemiptera* MANNHEIMS 1953 in Eastern Carpathians and an undescribed subspecies in Altai (OOSTERBROEK & THEOWALD 1992) and *T. invenusta subinvenusta* replaced by two subspecies: nominal subspecies in Scandinavia and Asia, and *T. i. microinvenusta* DUFOUR, 1990 in Sierra Nevada.

Five species living mostly at the lower subalpine level are also present in Scandinavia (*T. pallidicosta*, *T. subnodicornis*, *T. grisescens*, *T. gimmerthali* and *T. alpium*). All of these show no sign of speciation between Central Europe and Northern territories and have real boreo-alpine distribution. These species probably had their glacial refugium in the tundra zone separating both regions (Central Asian populations are known for *T. subnodicornis* and *T. grisescens* but are very isolated and can not have been the reservoir for the recolonisation of Europe). It is worth noting that subspecies are known only for *T. gimmerthali* in Southern Europe (*T. g. mattheyi* THEOWALD & DUFOUR 1983 in Pyrenees and *T. g. pteromaculata* THEOWALD, DUFOUR & OOSTERBROEK in Corsica, 1983).

On the contrary, an Asiatic origin is likely for *T. luridorostris* which has a large Eastern distribution and the biotope of which is coniferous forest or shrub zone. In a similar way some species listed by MANNHEIMS 1959 as boreo-alpine are in fact Asiatic species which after the Würm glacial period followed the extension of coniferous forests and reached Scandinavia as well as the Alps. Examples of such distributions may be found in *T. limbata*, *T. circumdata* which are high montane species. A similar origin will also explain the presence in the continental regions of Switzerland, at lower altitude, of other species such as *T. adusta* SAVTSIENKO 1954 and *T. bistilata* LUNDSTRÖM 1907.

All these examples show clearly how ecological requirements of species and historical factors are equally needed for biogeographical interpretations. The sequence of species in the alpine habitats and their ecological needs explain easily why certain species are endemic or localised in the mountains of Central Europe, why others are boreo-alpine and why still others of Asiatic origin could find in the Alps favorable conditions of development.

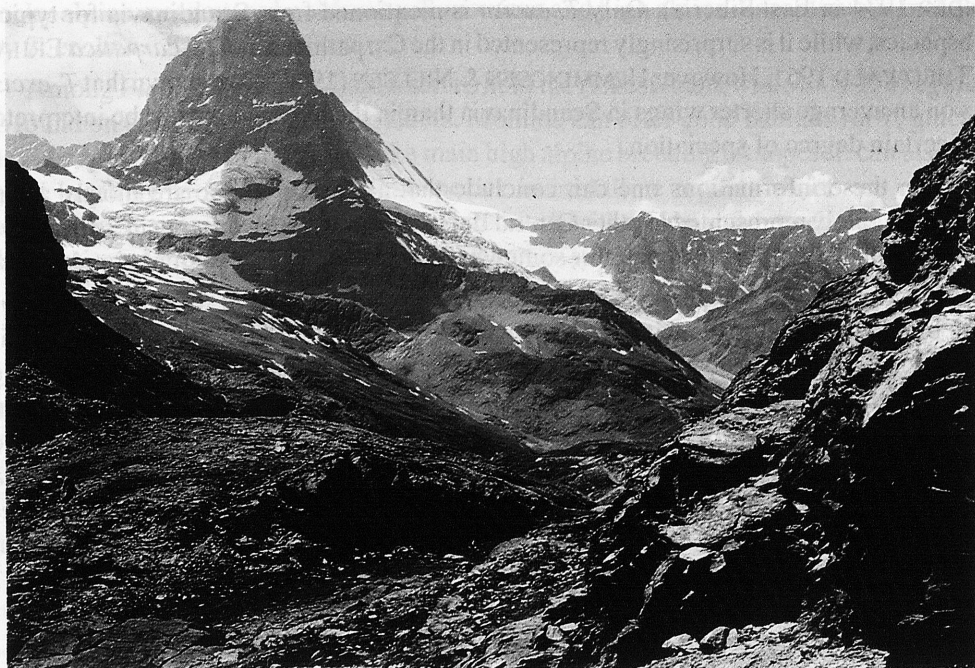


Fig. 1 Weathered rock with sparse and dry vegetation. Habitat of *T. sauteri* and *T. glacialis* (Rotenboden near Zermatt, 2800 m, TH 1).



Fig. 2 Sparse vegetation on limestone. Habitat of *T. glacialis* and *T. subglacialis* (Sanetsch, Valais, 2300 m, TH 1).



Fig. 3 Wet habitat of *T. subnodicornis* enclosed in alpine meadow with *T. excisa* on damper parts and *T. montana* on rocky grounds (Rotenboden near Zermatt, 2840 m, TH 1).



Fig. 4 Sequence of habitats on Munt Buffalora in Graubünden (2100-2630 m, TH 1-3). Coniferous forests (*T. h. strobliana*, *T. limbata*), subalpine meadows (*T. pallidicosta*, *T. cisalpina*), stream (*T. grisescens*), Pinus shrub zone (*T. austriaca*), alpine meadows (*T. excisa*, *T. montana*) and rock habitats (*T. glacialis*).

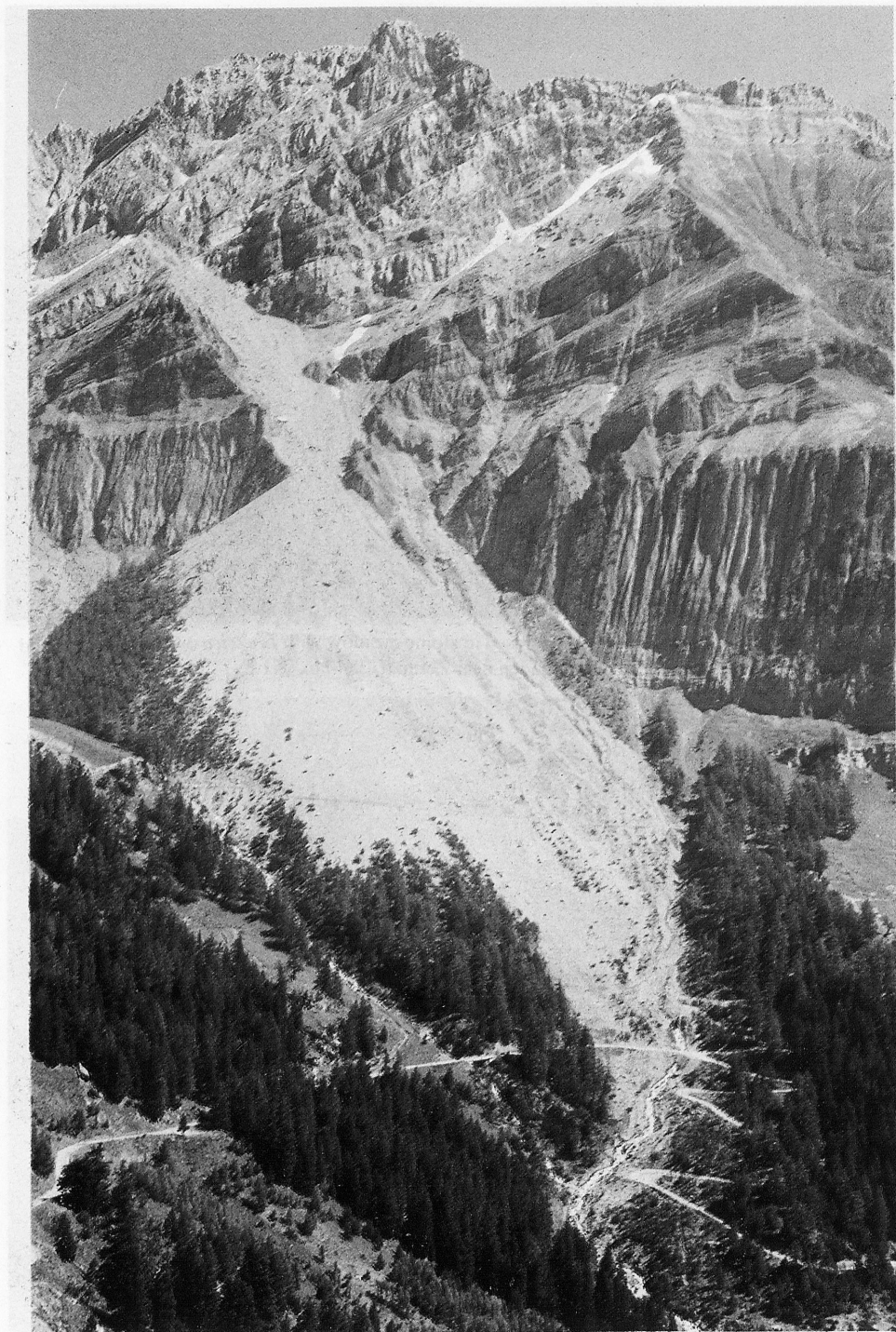


Fig. 5 Large screes cutting through subalpine zone. In sparse vegetation of lower part habitat of *T. subglacialis* at only 1750 m (Sanetsch, III 6).

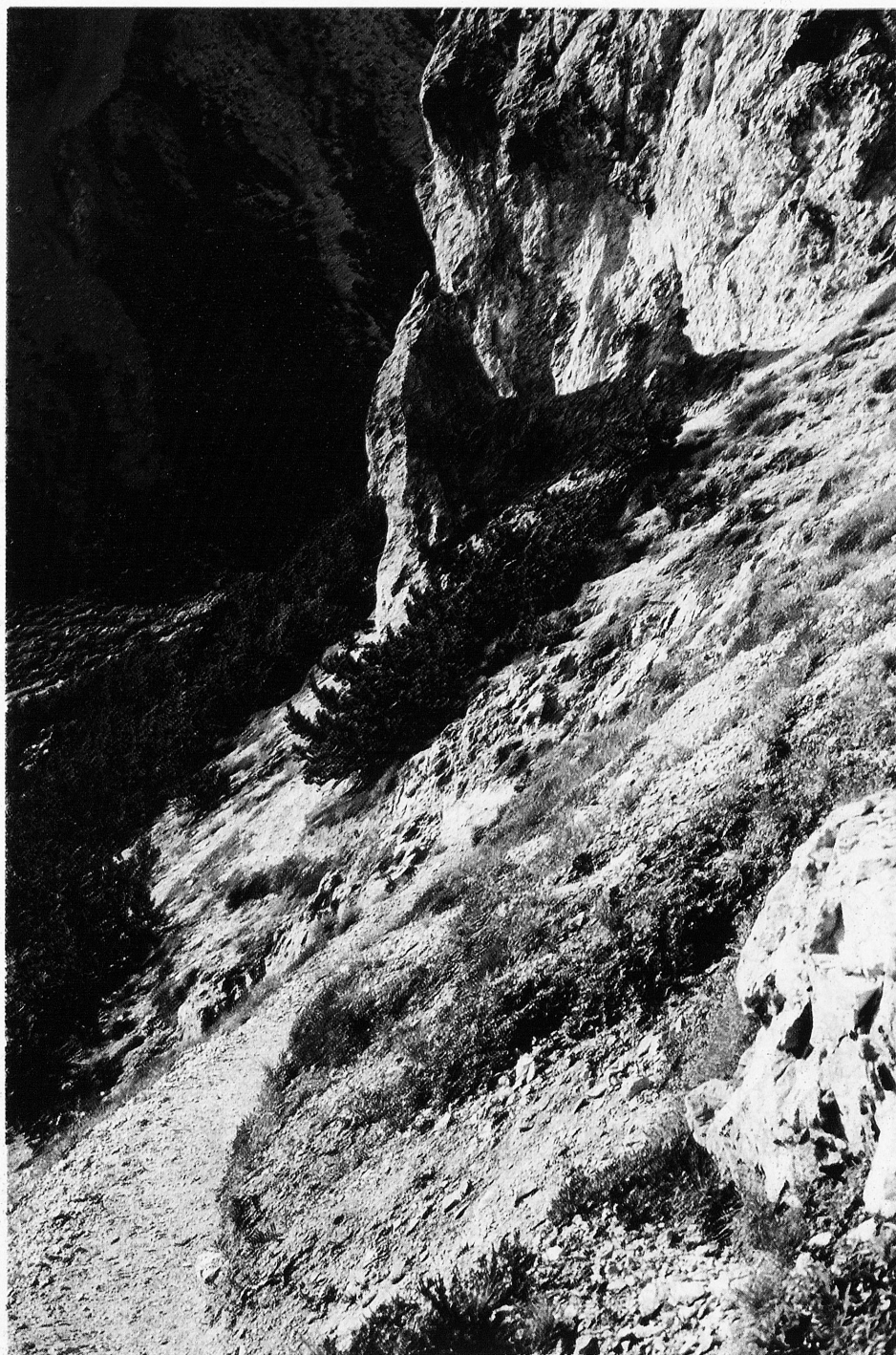


Fig. 6 Dry rocky habitat of *T. austriaca* and *T. mayerduerrii* with *Pinus* shrubs (Ofenpass, Graubünden, 2150 m, TII 3).

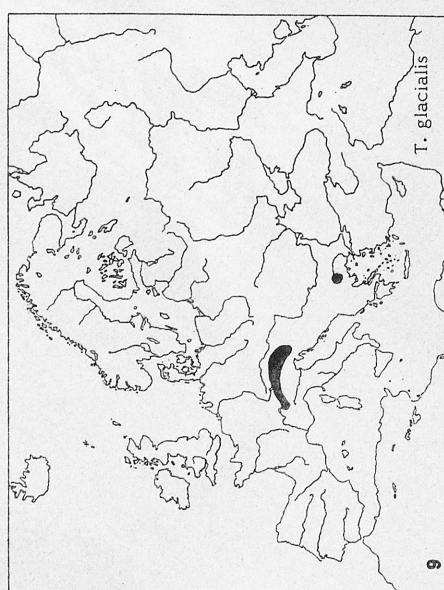
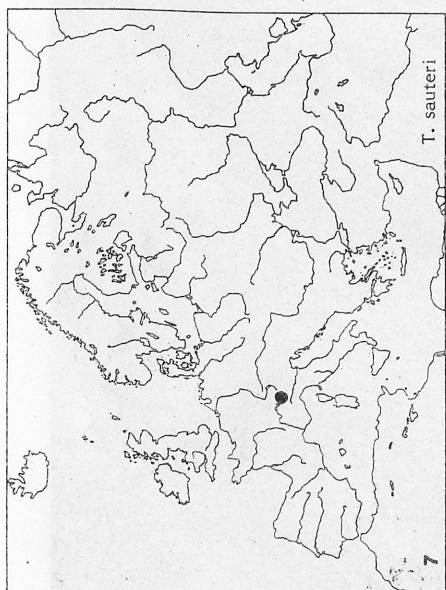
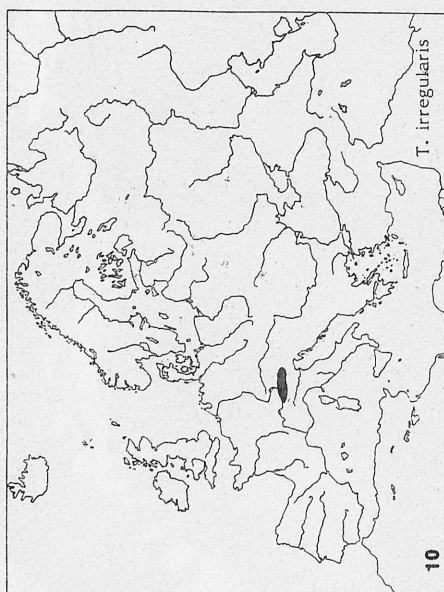
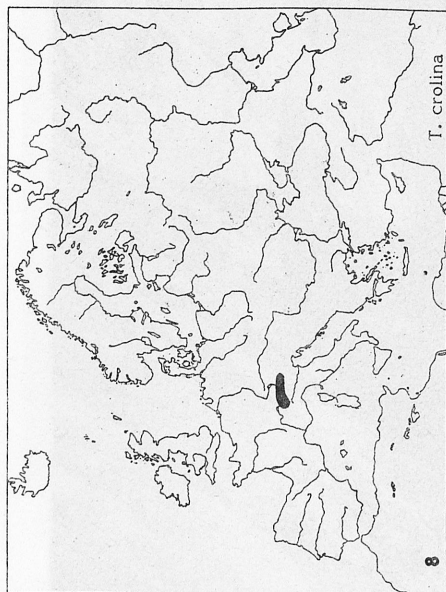


Fig. 8 *Tipula crolina*, alpine endemic.
Fig. 10 *Tipula irregularis*, alpine endemic.

Fig. 7 *Tipula sauteri*, alpine endemic.
Fig. 9 *Tipula glacialis*, Alps, Bulgaria (Rila).

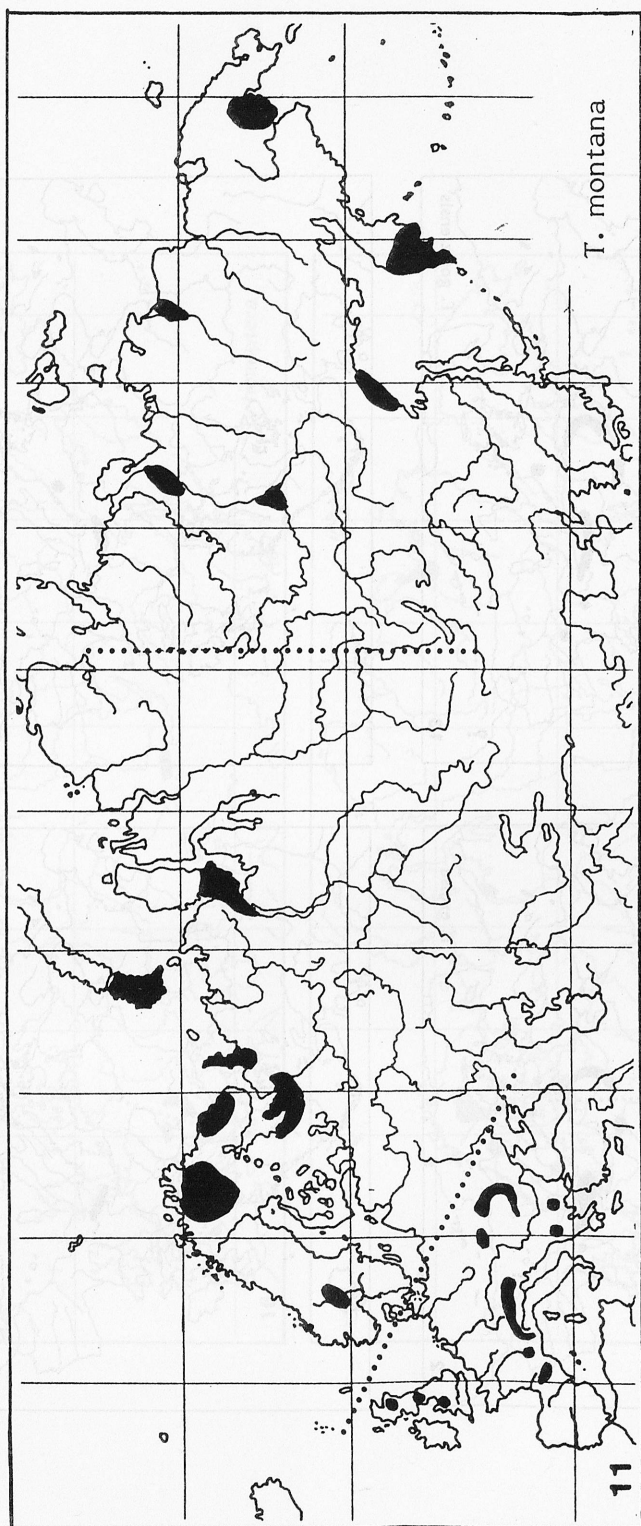


Fig. 11 *Tipula montana*: *m. montana* Curtis in Central Europe and Great Britain, *m. excisoides* in Eastern palaeartic, *m. verbernae* in North Western palaeartic.

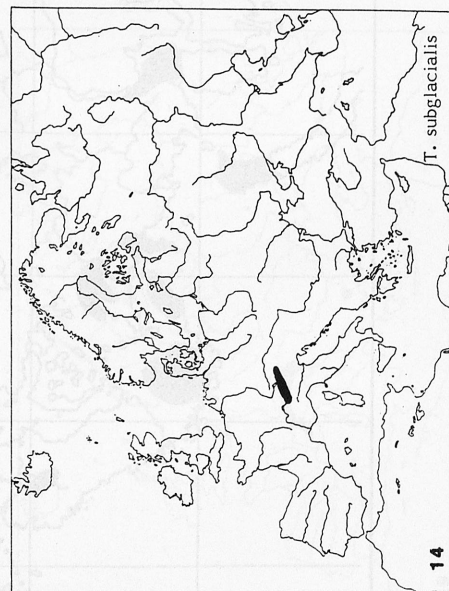
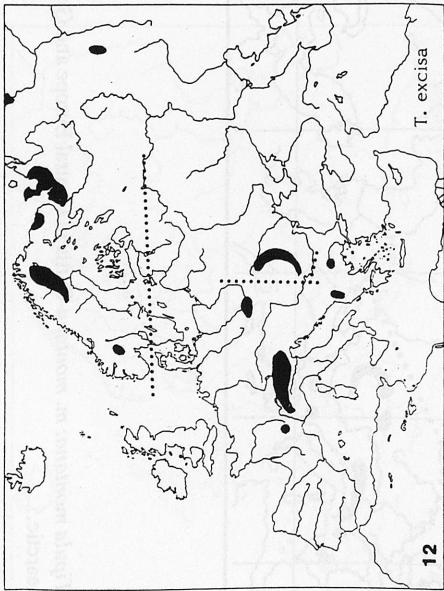
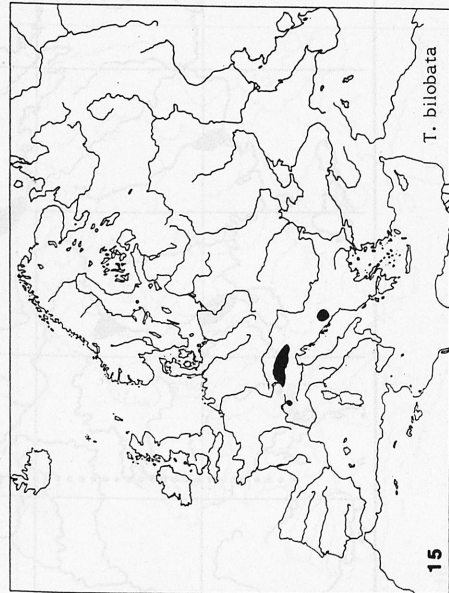
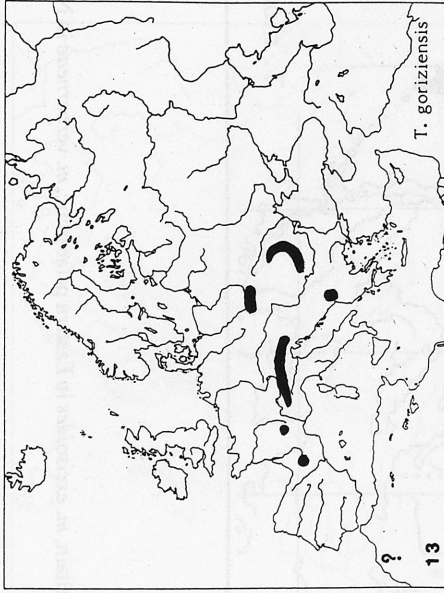


Fig. 13 *T. gorizensis*. Identity of North African specimens to confirm.

Fig. 15 *T. bilobata*, Alps and Balkan.

Fig. 12 *T. excisa*, subspecies *carpatica* in Carpathians; shorter winged populations in Scandinavia.

Fig. 14 *T. subglacialis*, alpine endemic.

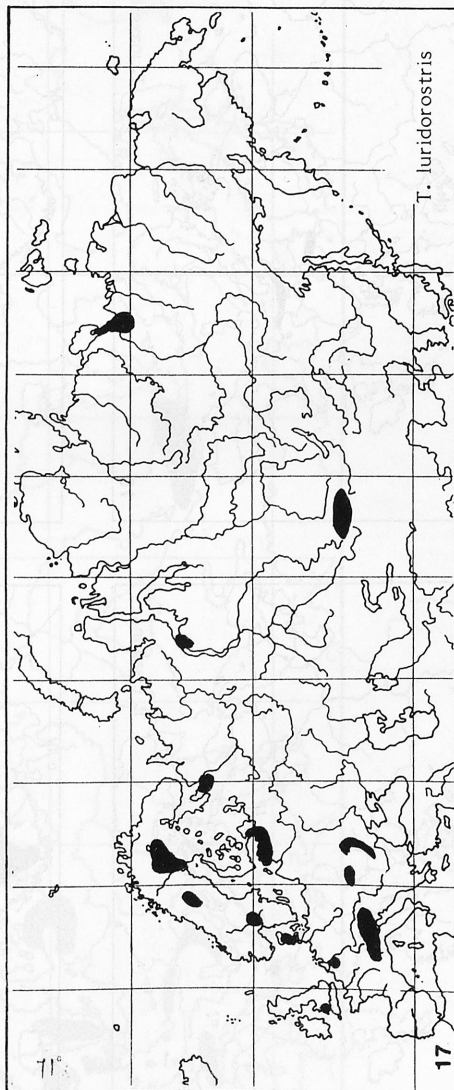
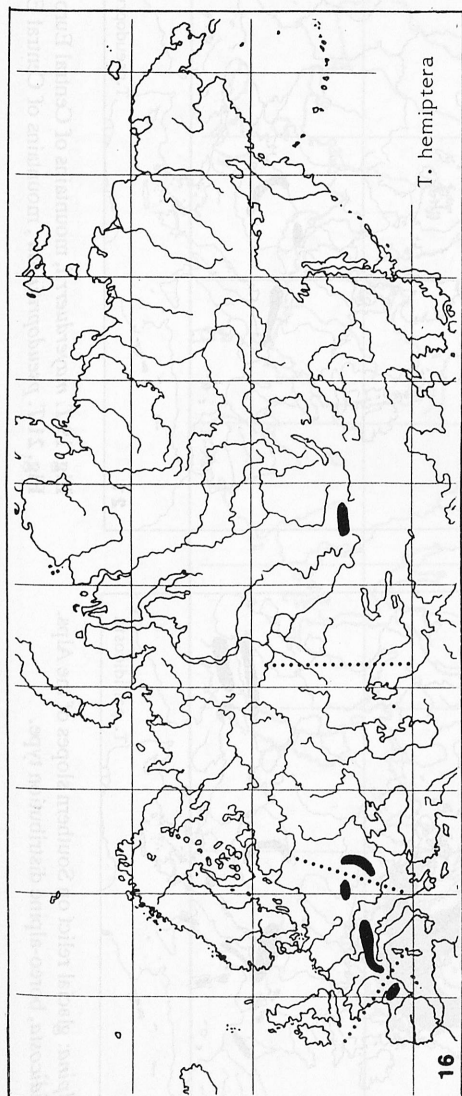


Fig. 16 *T. h. hemiptera* in Carpathians, *h. strobiliana* in Alps and Tatra, *h. pyrenaei* in Pyrenees and undescribed subspecies in Central Asia.
Fig. 17 *T. luridorostris*, wide Euro Siberian distribution.

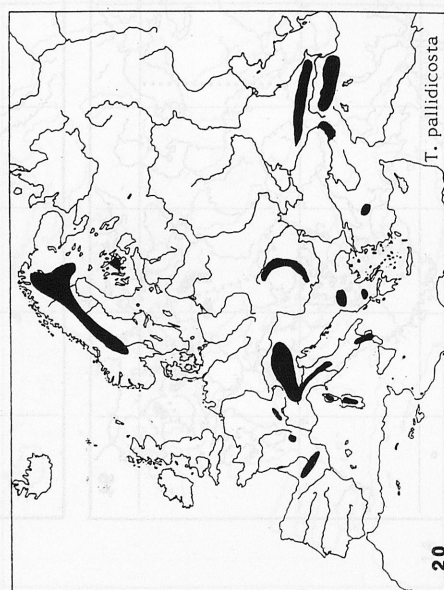
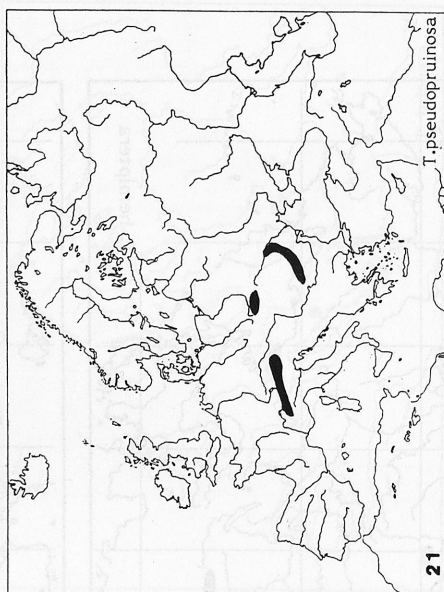
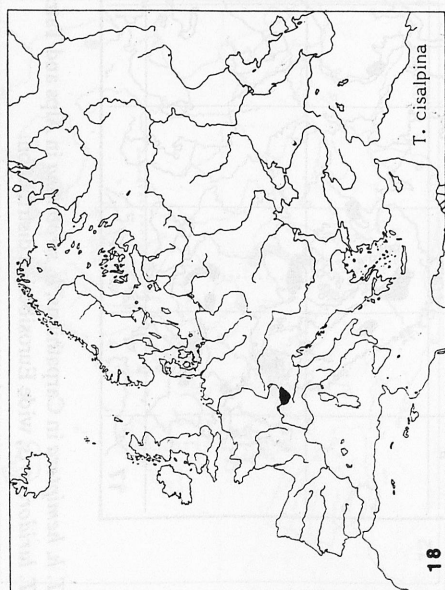
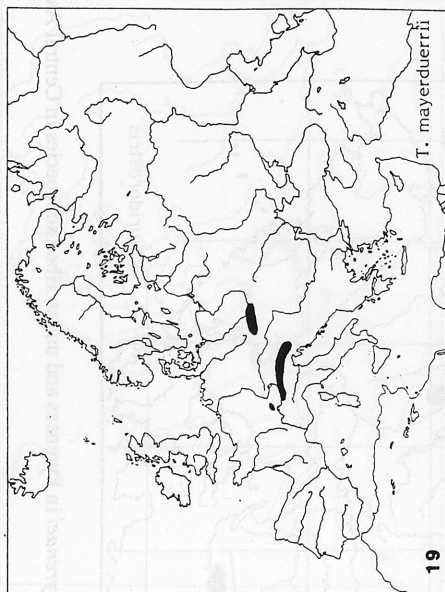


Fig. 18 *T. cisalpina*: glacial relict on Southern slopes of the Alps.
 Fig. 20 *T. pallidicosta*, boreo-alpine distribution type.

Fig. 19 *T. mayerduerrii*, mountains of Central Europe.
 Fig. 21 *T. pseudopruinosa*, mountains of Central Europe.

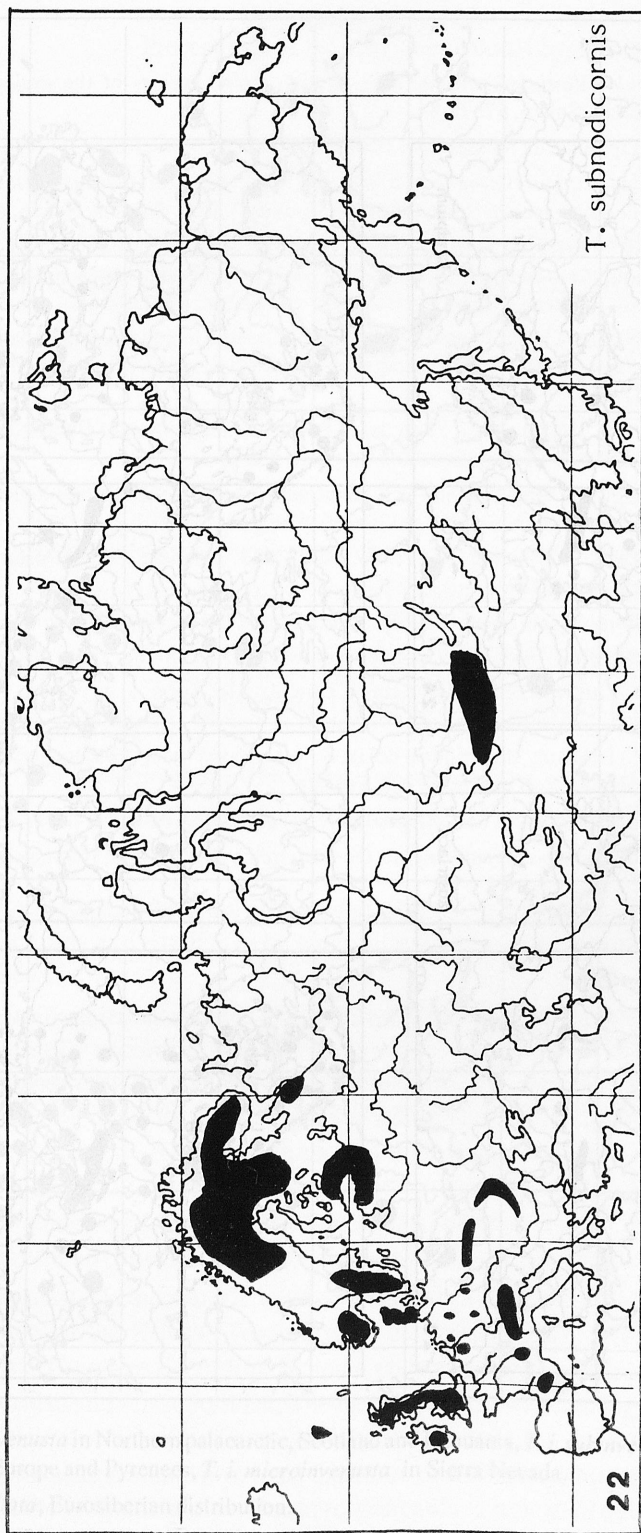


Fig. 22 *T. subnodicornis*, boreo-alpine distribution type. Isolated population in Central Asia.

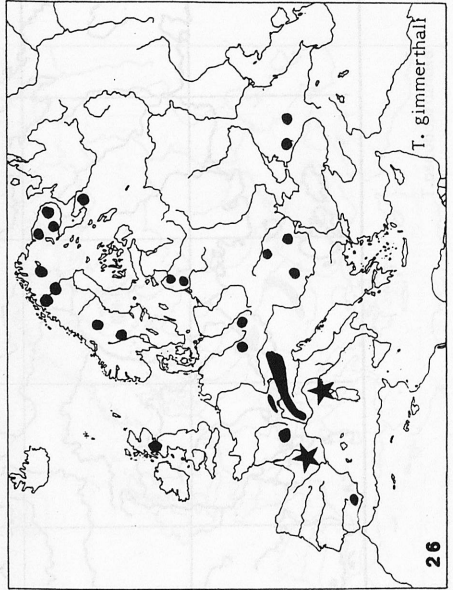
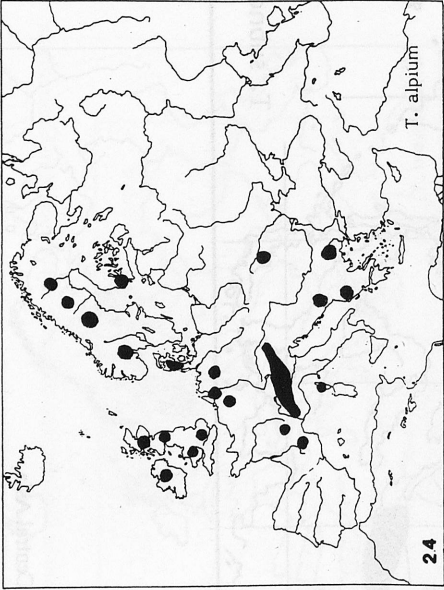
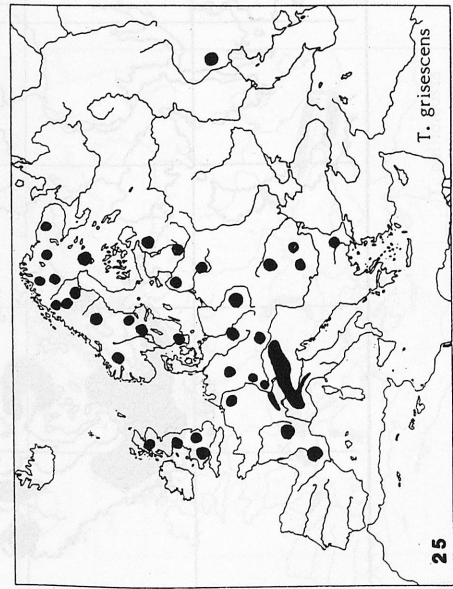
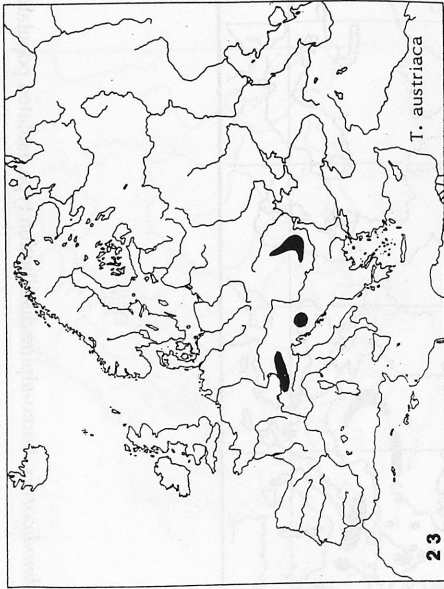


Fig. 23 *T. austriaca*, mountains of Central Europe.
Fig. 25 *T. griseus*, boreo-alpine distribution type.

Fig. 24 *T. alpinum*, boreo-alpine distribution type.
Fig. 26 *T. gimnerthali*, boreo-alpine. Localised subspecies in the South:
T. g. mattheyi in Pyrenees and *T. g. pteromaculata* in Corsica.

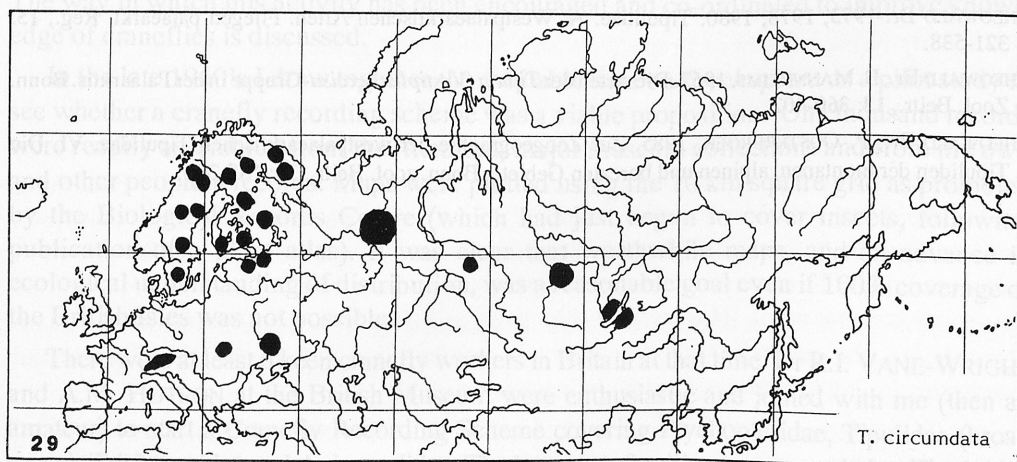
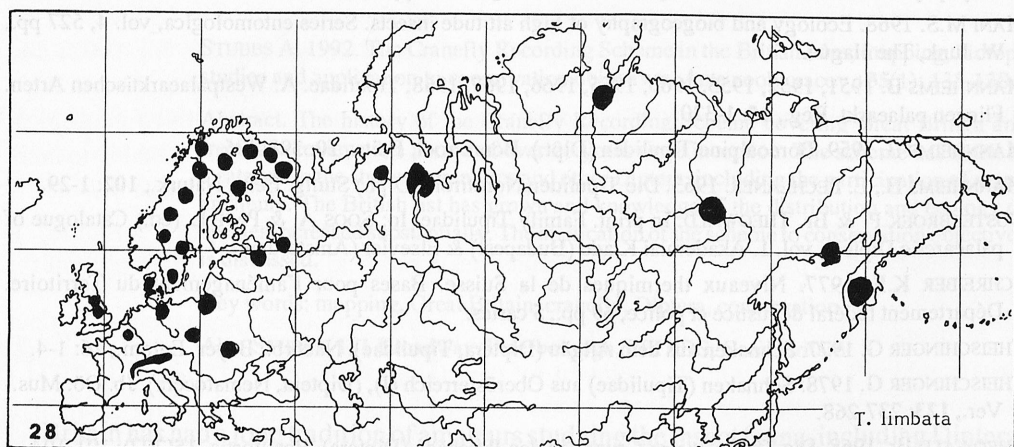
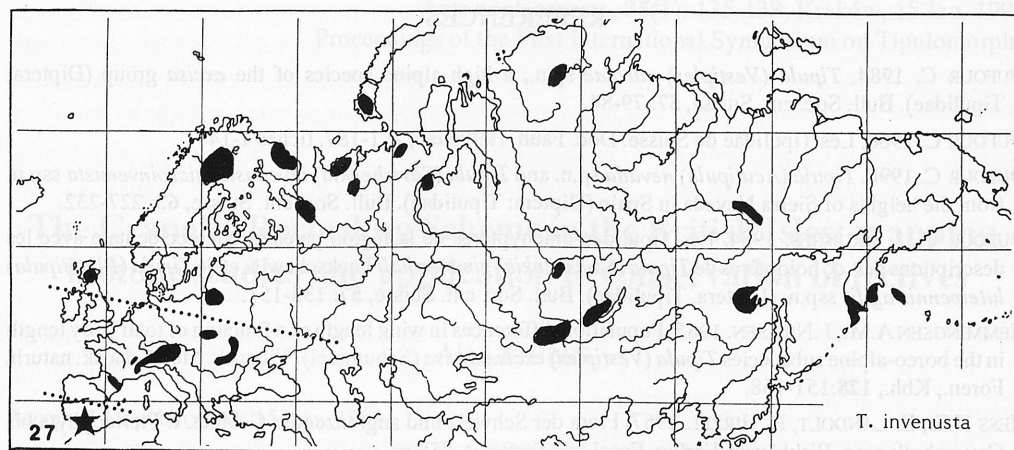


Fig. 27 *T. i. invenusta* in Northern palearctic, Scotland and Lithuania, *T. i. subinvenusta* in mountains of Central Europe and Pyrenees, *T. i. microinvenusta* in Sierra Nevada.

Fig. 28 *T. limbata*, Eurosiberian distribution.

Fig. 29 *T. circumdata*, Eurosiberian distribution.

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