

ALLOZYMIC AND MORPHOLOGICAL VARIATION IN *EPHIPPIGER TERRESTRIS* (YERSIN, 1854) (INSECTA, ORTHOPTERA, TETTIGONIOIDEA)

by

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ABSTRACT

Landman, W., L. Oudman, & M. Duijm, 1989. Allozymic and morphological variation in *Ephippiger terrestris* (Yersin, 1854) (Insecta, Orthoptera, Tettigonioidea). – Tijdschrift voor Entomologie 132: 183-198, figs. 1-13, tabs. 1-11. [ISSN 0040-7496]. Published 1 December 1989.

Based on allozyme frequencies the genetic distances between seventeen populations of *Ephippiger terrestris* are determined and compared with biometrics of epiproct, cerci and titillators. The distinction of three subspecies, viz. *terrestris*, *bormansi* and *caprai* is confirmed. As a result of the large variability of all characters within populations, distinction between subspecies generally is not sharp. At the boundaries of the species distribution area the subspecies characters are clearest, whereas in the centre an extensive area with intermediate populations is present, generally exhibiting clinal differences. Such gradients are described for several characters for a number of populations along a transect near Tende in the French Alps.

Key words. – *Ephippiger terrestris*, subspecies, biosystematics, enzyme electrophoresis, male appendages, intermediates, clines.

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INTRODUCTION

Ephippiger terrestris (Yersin, 1854) occurs in the French Alps, in the neighbouring Italian Alps and also around the Italian-Swiss lakes. Nadig (1980) argued that *E. bormansi* (Brunner von Wattenwyl, 1882) has to be regarded as a subspecies of *E. terrestris* and described a new subspecies, *E. t. caprai*. Furthermore, he found intermediates between *E. t. terrestris* and *E. t. bormansi* in a broad area in the department Alpes Maritimes (Fig. 1). Duijm and Oudman (1983) confirmed these results; they showed that between *bormansi*, *caprai* and *terrestris* no mating barriers occur. Mating attempts between these *terrestris* subspecies and *E. ephippiger* failed, however, apparently due to differences in cerci and epiproct in the male and the place of the copulatory sockets in the female partner. Hartley and Warne (1984) confirmed these findings by measurements of male cercal reach and the corresponding female inter-socket distances.

In this study morphometric characters are in-

vestigated, primarily to consider the relations between the three subspecies mentioned and the position of intermediates, mainly from a transect near Tende. Allozyme analysis is used to get an independent character set. The allozyme frequencies in *E. terrestris* are compared with those in *E. ephippiger vicheti*, the latter being chosen as it occurs sympatrically with *E. t. bormansi* at site 14 near the Lago di Como.

MATERIALS AND METHODS

Collection. – Specimens were collected during field trips in 1980 and 1981. For locations see table 1 and figs. 1 and 2. In 1981 special attention was given to a transect near Tende (sites 1-11), where intermediates might be found according to Nadig (1980) and our own preliminary observations in 1980. The collecting area varied from one to several acres, depending on the population density. The animals were killed, measured, photographed and frozen in solid carbondioxide (-79°C) within one day of capture.

Table 1. Collection sites of *Ephippiger* species.

No.	Location	Country/dept.	Altitude (m)		Date
<i>Ephippiger terrestris</i>					
1.	Mézel/Majastres	F 04	1200	A)	20-viii-80
				B)	24/28-viii-81
2.	Col de Maure	F 04	1350		24-viii-81
3.	Gréolières/Plan de Peyron	F 06	1100		29-viii-81
4.	Col de Braus	F 06	1000		30-viii-81
5.	Col de Castillon	F 06	700		31-viii-81
6.	Cle. Scravaion	It Liguria	820		3-ix-81
7.	Tende	F 06	830	A)	29/31-viii-80
				B)	1/3-xi-81
8.	Vievolà 1	F 06	915		2-ix-81
9.	Vievolà 2	F 06	1050		2-ix-81
10.	Col de Tende 1	F 06	1200		2/5-ix-81
11A.	Col de Tende 2	F 06	1400		2-ix-81
11B.	Col de Tende	F 06	1350/1420		30-viii-80
12.	Col de Tende 3	F 06	1600		2-ix-81
13.	Vallone del Arma	It Piemonte	1600		31-viii-81
14A.	Naggio (L. di Como)	It Lombardia	800		5/6-ix-81
15.	Mt. Grona (Lago di Como)	It Lombardia	1400		6-ix-81
17.	Collobrières	F 84	135		26-viii-80
18.	Fayence	F 84	250		28-viii-80
19.	Aiguines (Verdon)	F 84	850		23-viii-80
<i>Ephippiger ephippiger vicheti</i>					
14B.	Naggio (L. di Como)	It Lombardia	750		5/6-ix-81
16.	Migliaglia/Mt. Lema	CH Ticino	720		7-ix-81

Electrophoresis. – Preparation of samples, electrophoretic techniques and the preparation of the horizontal polyacrylamide gells were carried out as in Van Dijk & Van Delden (1981). The following eighteen enzyme loci were analysed: Alcohol dehydrogenase (Adh), Tetrazolium oxidase (To), two Phosphoglucumutases (Pgm-2 and -3), three Esterases (Est-1, -2 and -5), Aldehyde dehydrogenase (Aldox-2), two Hexokinases (Hk-2 and -3), Fumarate hydratase (Fum), Xanthine dehydrogenase (Xdh), Glucose oxidase (Gluo-3), Aldolase (Ald), Malic enzyme (Me), Isocitrate dehydrogenase (Idh), α -Glycerophosphate dehydrogenase (α -Gpdh) and Glycerine dehydrogenase (Glydh).

A preliminary electrophoretic survey was made in 1980 (Landman 1981). In this study ten of the above mentioned loci were examined for *E. terrestris* from six localities (Nos. 1, 7, 11B, 17, 18 and 19). For polymorphic loci Mendelian inheritance was assumed on the basis of enzyme band patterns and checked by testing genotype frequencies for every location for Hardy-Weinberg equilibrium.

Between populations Nei's genetic distances were calculated (Nei 1975). From the matrix of genetic distances a dendrogram was constructed according to the UPGMA method (Sneath and

Sokal 1973). Principal component analysis was carried out with the allele frequencies (arcsin \sqrt{p} transformed). The principal component scores of each population were calculated and the first and second represented in a diagram.

Morphology. – Five characters of body and legs were measured in the field: body weight (BW), body length (LB), length of pronotum (LP), length of hind femur (LF) and length of fore tibia (LT). Weight was determined by means of a Pesola pocket spring balance (0 – 5 g in 0.1 g). Length was measured with sliding calipers. In a number of samples one character of the pronotum and one of the head was scored. Nadig (1980) distinguished a shield-shaped field medially in the metazona of the pronotum and named it *campus medianus*; he showed that the lateral limitation of this field is sharper in *E. t. bormansi* than in *E. t. terrestris* and *E. t. caprai*. Moreover, this field is smooth in *E. t. bormansi* and more or less granular in the other subspecies. We scored the surface texture with: 0 – smooth, 1 – granular, and 2 – rough, but we did not find the latter character-state represented in our samples. Furthermore we paid attention to the "fastigium verticis" on the head, the profile of which, according to Nadig (l.c.) varies from very

steep to receding, a steep fastigium being characteristic for *E. t. bormansi*. We scored: 0 – steep, 1 – rather steep, 2 – receding.

Colours of pronotum and abdomen were also noted in the field.

Cerci and epiproct of freshly killed specimens were photographed with a Medical Nikkor (2 : 1). From the projected diapositives drawings with an end magnification of 40x were made. Measurements were carried out on these drawings. To characterise the form of the epiproct the following dimensions were measured (fig. 3A): apical, central and basal width (EA, EC and EB, respectively), lateral and medial length (EL and EM).

Fig. 3B shows the way in which the cerci were measured: total length (CL = CA + CB) and its division by the place of the inner tooth in length of apex (CA) and basal length (CB), basal width (CE) and apical width (CF) and finally, a measure (CD) for the form of the outer lateral side of the cercus, CD taken negative when this side is convex and positive when concave.

Titillators were removed from the body and measured with a stereomicroscope (20x) using an ocular micrometer. Figure 3C shows the way in which they were measured. TL indicates the total length of the apical part of the titillator, TT the length of the toothed part of it and TN the number of teeth. The width of the apical part is measured as TA, so that the ratio TA/TT indicates its slenderness.

Samples of collected specimens from all localities, including tips of abdomens of the specimens used for electrophoresis, will be deposited in the Entomological collection of the Institute for Taxonomical Zoology (Zoological Museum) in Amsterdam.

RESULTS

Allozymes

Eighteen loci were surveyed of which six were polymorphic: Pgm-2, Pgm-3, Est-1, Est-2, Est-5 and Adh, with 3, 5, 2, 4, 2 and 2 alleles, respectively.



Fig. 1. Collection sites and distribution of *Ephippiger* species in S. France, S. Switzerland and NW. Italy.

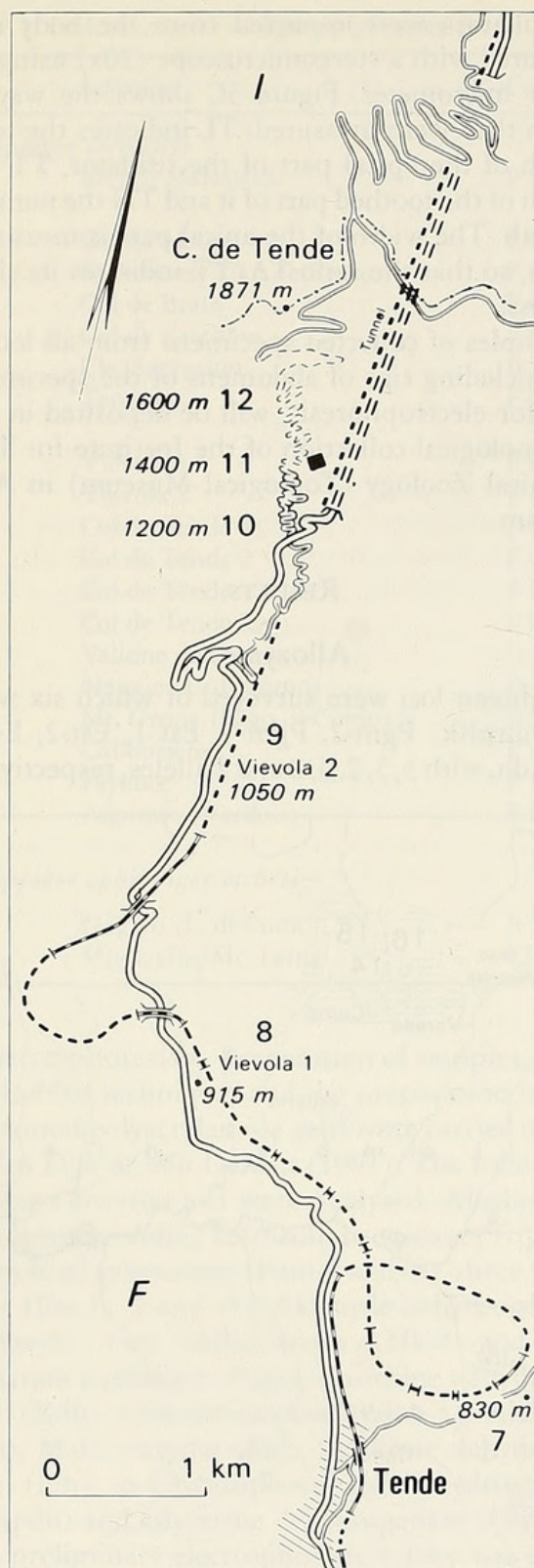


Fig. 2. Collection sites along the Tende transect (locations 7-12) in Southeast France.

The allozyme frequencies are shown in table 2. The genetic distances are summarized in table 3 and the dendrogram calculated from these distances is given in fig. 4.

The aggregate of all *E. terrestris* populations

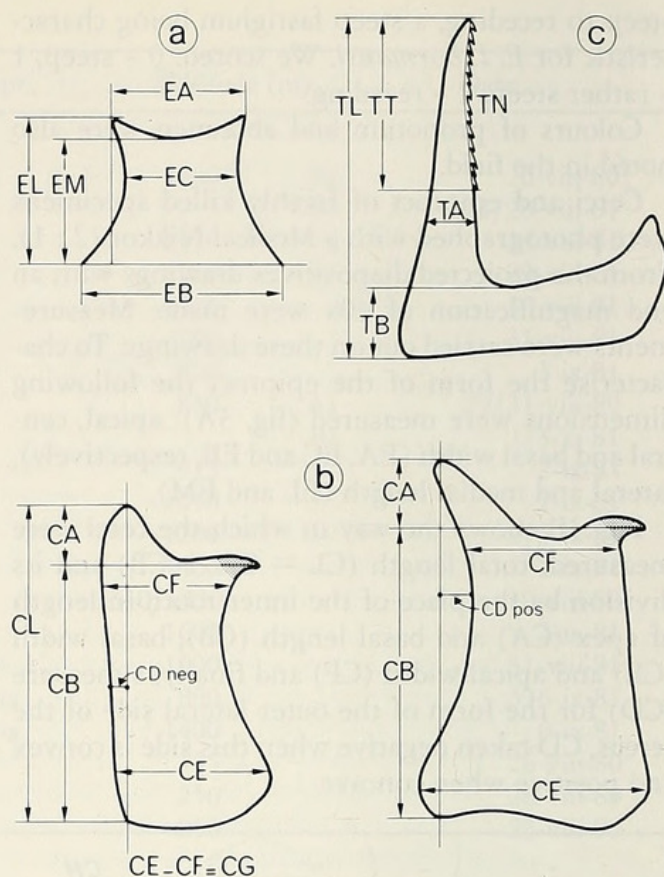


Fig. 3. Method of measurement of (a) epiproct, (b) cerci, (c) titillators. For abbreviations see text.

appears to be well separated from *E. ephippiger vicheti* (distance 0.1713). For *E. t. caprai* the separate position is also clear. The distance between *E. t. bormansi* and *E. t. terrestris* is less. The populations along the Tende transect together form a separate group.

The results of the 1980 study – as far as *E. terrestris* is concerned – are summarized in table 4, in which the distances for six populations are given. In these data the sites 17 and 18 represent with certainty the nominate form, whereas this may be doubted with regard to the site 5 in the former series. The 1980 and 1981 distances are combined in the semi-geographical representation of fig. 5. Comparison of these data appears to be justified, because the distances between the populations 1 and 7, determined both in 1980 and 1981, were quite similar: 0.0742 and 0.0785 respectively.

Principal component analysis was carried out for 14 populations of *E. terrestris* and for 18 allozymes. Fig. 6 shows the relation between the principal components 1 and 2. PC 1 and PC 2 together explain 55% of the total variance. The distribution of the 14 populations in this diagram is similar to their position in the dendrogram (fig. 4), though the methods used are quite different.

Morphology

The measurements of body and legs are summarized in table 5. The means of these measurements are generally linearly interrelated as appears from table 6. By way of illustration the relation between body weight and body length is shown in fig. 7. The *E. t. bormansi* populations are on average the smallest ones, even smaller than our *minor* samples. Specimens of the nominate form, represented by the localities 17 and 18 and perhaps also no. 5 (Col du Castillon) are the biggest ones. *E. t. caprai* occupies an intermediate position and the samples along the Tende transect are intermediate between *caprai* and *bormansi*.

Table 7 shows that the mean body measurements are negatively correlated with the altitude of the collection site; especially for LT and LF the correlation is rather close. This is illustrated in fig. 8 for the relation between LT and altitude. The distribution of the samples is rather similar to that in fig. 7, only the mean length of the tibia in Naggio (No. 14A) is too short for the altitude of this site.

To compare the form of the epiproct in the various populations only mean ratios are used (table 8) and not absolute measurements, because these strongly depend on body dimensions. The variation in the ratios EL/EM and EA/EC is represented in the diagram of fig. 9. The three subspecies *caprai*, *terrestris* and *bormansi* appear to be well separated. In the nominate subspecies EL/EM is larger than in the other two subspecies. This means that the hind margin of the epiproct is bent

inside so that the hind corners are protruding. The ratio EL/EM in *bormansi* is the same as in *caprai*, and significantly smaller than in *terrestris*, indicating that the hind corners are not prolonged and may even be rounded. There is a clear difference in the ratio EA/EC between *bormansi* and *caprai*: the higher value in *bormansi* points to the often laterally projecting hind corners, whereas the low value in *caprai* indicates the rounded hind corners of the epiproct in this subspecies. The forma *minor* has the same high EL/EM ratio as the nominate form, whereas its EA/EC ratio is higher. So in the mean the hind corners are in *minor* somewhat more laterally protruding than in the nominate form; in this respect *minor* resembles *bormansi*.

Our measurements of the cerci are summarized in table 9. Cercal dimensions are correlated with the dimensions of other parts of the body. The mean total length of the cercus (CL) is moderately correlated with mean length of the tibia ($r = 0.486$), the measurements CD and CE closely ($r = 0.916$ and 0.949 , respectively). Therefore we characterize the cercal form by means of the ratios. In fig. 10 the relative length of the apex (CA) is compared with the relative deviation of a straight outer margin (CD). The nominate form has the longest apical part and a strongly concave outer margin. *E.t. bormansi* has a shorter apical part and a slightly convex outer margin. *E.t. caprai* has a rather short apical part and a slightly concave outer side. The forma *minor* is intermediate between *t. terrestris* and *t. bormansi*, the populations along

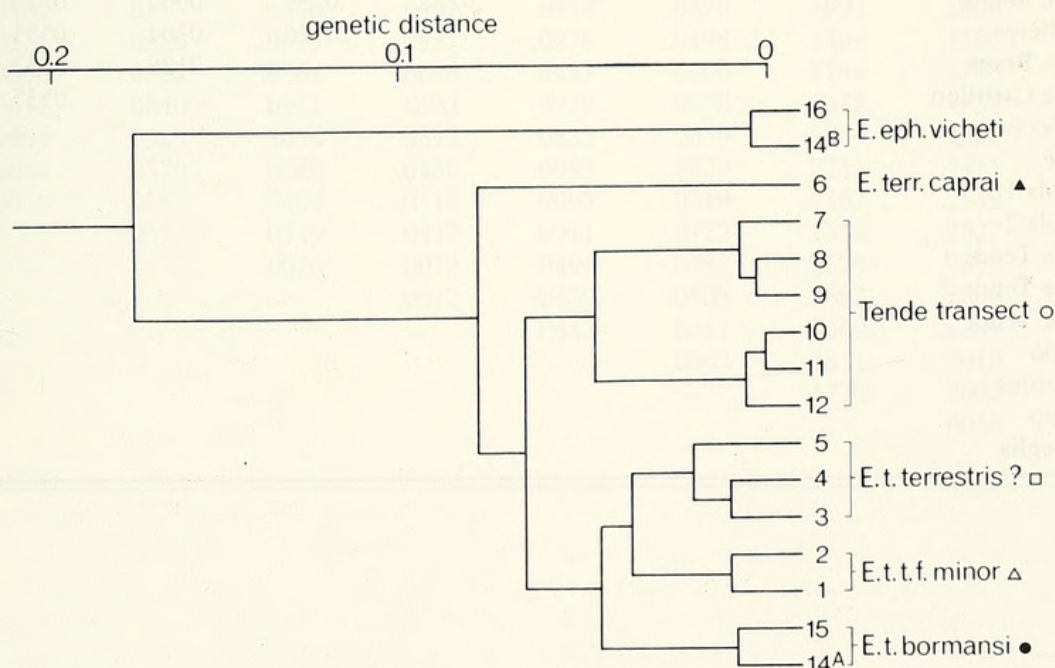


Fig. 4. Dendrogram of *Ephippiger terrestris* populations, based on genetic distance, calculated from table 3 (1981 data).

Table 2. Allozyme frequencies of *Ephippiger* populations (n.m. = not measured).

No.	Locality	n	Pgm-2			Pgm-3				
			a	b	c	a	b	c	d	e
<i>E. terrestris</i>										
1B.	Mézel/Majastres	28	.38	.62	-	-	-	.91	.09	-
2.	Col de Maure	13	.23	.77	-	-	-	.69	.31	-
3.	Gréolières	20	.50	.40	.10	-	.25	.38	.38	-
4.	Col de Braus	20	.43	.40	.18	-	.39	.33	.28	-
5.	Col de Castillon	18	.50	.50	-	.27	.67	-	.07	-
6.	Cle. Scravaion	23	.28	.65	.07	-	.96	.04	-	-
7.	Tende	20	.10	.90	-	-	.60	.40	-	-
8.	Vievola 1	20	-	1.00	-	-	.70	.25	-	.05
9.	Vievola 2	16	-	1.00	-	-	.69	.31	-	-
10.	Col de Tende 1	15	-	1.00	-	-	.11	.79	.05	.05
11.	Col de Tende 2	7	-	1.00	-	-	-	1.00	-	-
12.	Col de Tende 3	8	-	1.00	-	-	-	.88	-	.13
14A.	Naggio	18	.69	.31	-	-	-	1.00	-	-
15.	Mt. Groma	10	.60	.40	-	-	.10	.80	.10	-
<i>E. e. vicheti</i>										
14B.	Naggio	21	1.00	-	-	1.00	-	-	-	-
16.	Miglieglia/Mt. Lema	18	1.00	-	-	1.00	-	-	-	-

Table 3. Genetic distances between populations of *Ephippiger* species.

No.	Localities	<i>E. terrestris</i>						
		1B	2	3	4	5	6	7
1B.	Mézel/Majastres	-	.0102	.0243	.0276	.0555	.0822	.0785
2.	Col de Maure		-	.0253	.0299	.0604	.0829	.0540
3.	Gréolières			-	.0126	.0304	.0555	.0627
4.	Col de Braus				-	.0128	.0637	.0611
5.	Col de Castillon					-	.0535	.0779
6.	Cle. Scravaion						-	.0823
7.	Tende							-
8.	Vievolà 1							
9.	Vievolà 2							
10.	Col de Tende 1							
11.	Col de Tende 2							
12.	Col de Tende 3							
14A.	Naggio							
15.	Mt. Groma							
14B.	Naggio							
16.	Migliaglia							

Table 4. Genetic distances, calculated from allozyme frequencies determined by Landman (unpublished) for six samples of *Ephippiger terrestris* collected in 1980.

No.	Location	17	18	19	1A	11B	7
17.	Collobrières	-	.0233	.0634	.0482	.0789	.0709
18.	Fayence		-	.0278	.0477	.0553	.0912
19.	Aiguines			-	.0480	.0518	.1090
1A.	Mézel/Majastres				-	.0341	.0742
11B.	Col de Tende					-	.1247
7.	Tende						-

the Tende transect are approximately intermediate between *t. caprai* and *t. bormansi*. Strikingly apart is the position of the populations 4 and 5 owing to their relatively very short apices.

The basal part of the cercus tapers somewhat towards the apex; this tapering is measured by CG, the difference between CE and CF. Figure 11 shows the relative measure of tapering. This is least in *bormansi* and strongest at the sites 4 and 5. The nominate and the *minor* form occupy an intermediate position, as does *caprai*. The three sites at the Col de Tende (10 – 12) are intermediate between *terrestris* and *bormansi*.

According to Nadig (1980) the apical parts of the titillators vary in slenderness. Our observations

(Table 10) confirm this statement; we determined the ratio TL/TA for *caprai* at 5.8, whereas the values for the three *bormansi* sites were 11.8, 10.5 and 12.2 (mean 11.5). The *bormansi* titillators are therefore evidently more slender than those of *caprai*. Those of the forma *minor* were similar to *bormansi*. Along the Tende transect we found for the sites 7 – 12 the ratios 6.4, 6.9, 8.05, 10.7, 11.0 and 10.7 respectively. So there is a clear gradient between *caprai* and *bormansi*, respically along the first part of the transect.

The relative scores for the texture of the campus medianus and the form of the fastigium verticis are shown in fig. 12. With regard to the campus medianus (fig. 12A) the character states as specified by

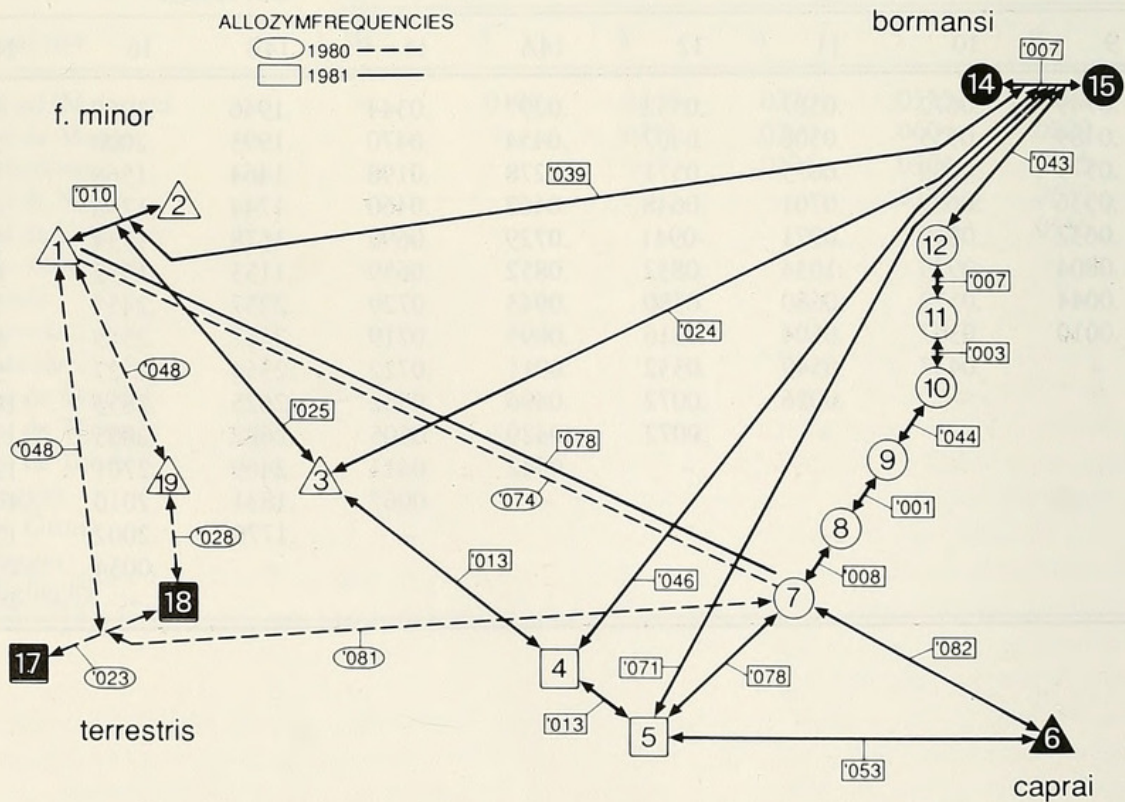


Fig. 5. Semigeographical representation (not on scale) of genetic distances between adjacent populations of *Ephippiger terrestris* (1981 and 1980 data).

Nadig (l.c.) are clearly confirmed: the surface is smooth on sites 13 and 14 and therefore in *bormansi*, whereas the granular state is apparently characteristic for *caprai* (sites 6–9). The situation at the three sampling sites along the Col de Tende (10–12) is intermediate with the *bormansi* state prevailing at sites 11 and 12, whereas at site 10 the *caprai* state predominates, indicating a rather steep transition with regard to this character over an altitude difference of 200 m.

The steepness of the fastigium verticis shows also a gradual transition (fig. 12B). A steep fastigium appears to be characteristic for *E. t. bormansi* and a less steep or even receding one for *E. t. caprai*; a transitional situation is found along the Tende transect.

It has to be stressed that all the above morphological results have been obtained by using the means of rather variable series of measurements; the statements do, therefore, not necessarily apply to the form of the various parts in individuals belonging to the populations studied.

Figure 13 gives an overall picture of the colour of the abdomen. The various shades noted were here combined into three categories only, viz. green, brown and grey. The predominance of grey (in fact yellowish grey) in the nominate form (sites 17 and 18) is remarkable. At other places shades of green and brown were most common, whereas grey was rather rare. There appears to exist a gradient along the Tende transect with the percentage of green individuals changing from 100% to 45%. Table 11 gives a more detailed picture of this situation by also giving the shades of green observed. One sees that in *caprai* (site 6) only plain-green specimens were found, whereas at the sites along the transect other shades of green occurred, though in small numbers. The decrease of the relative numbers of plain-green specimens along the transect is obvious. In the same time the occurrence of three rows of dark spots on the abdomen (a *bormansi* character) increases along this transect, as appears from Table 11. Very interestingly also at site 3 a sizeable percentage of this character was observed (32%, $n = 28$).

DISCUSSION

As typical representatives of the nominate form, *E. t. terrestris*, we consider our samples from Fayence (18) and Collobrières (17) from the lower parts of the department Var. Here one finds the biggest specimens. The epiproct usually has markedly protruding hind corners. The cerci have a long apex, a concave outer margin and the basal part tapers somewhat towards the apex. Unfortun-

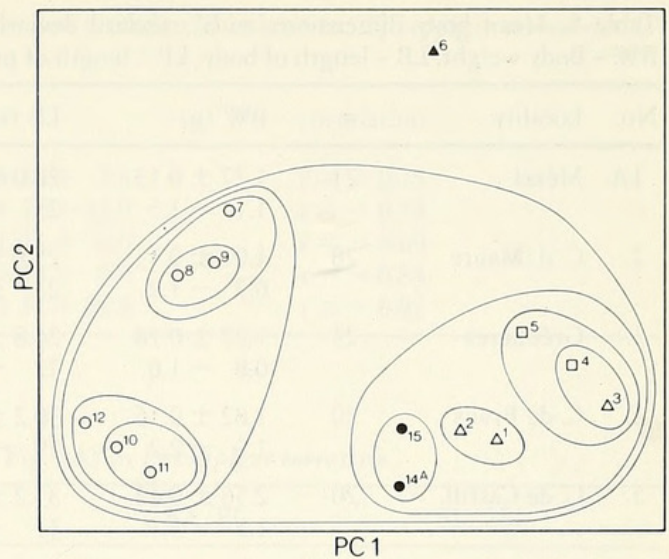


Fig. 6. Diagram of scores for Principal Components 1 and 2, based on allozyme frequencies for 14 locations of *Ephippiger terrestris*.

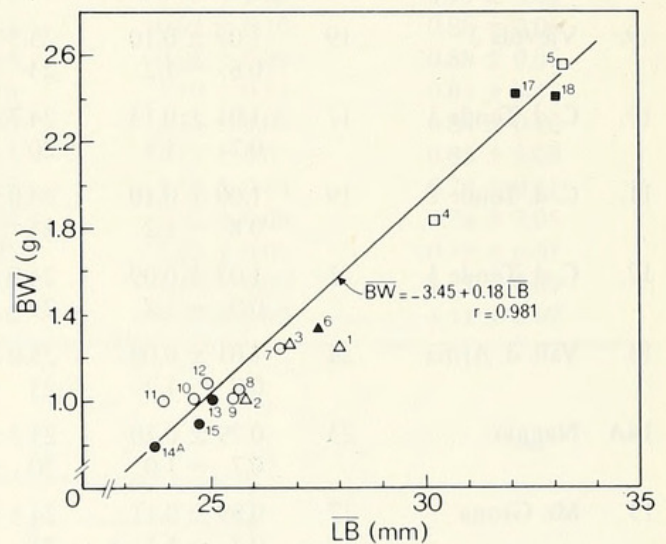


Fig. 7. The relation between mean body weight (BW) and mean length of body (LB) in *Ephippiger terrestris*.

nately these populations are missing in our 1981 collections. The 1980 data indicate a distance $D = 0.048$ to the *minor* population of site 1.

Nadig (1980) described *E. t. caprai* as a new subspecies from the Ligurian Alps, close to *E. t. terrestris*, but differing in form of epiproct and titillators and in colour; the fresh grassgreen body-colour is an important character in living *caprai* specimens. For the *caprai* population studied we can confirm his results: epiproct with rounded corners, titillators with rather thick apical part. Moreover, our results indicate differences in the form of the cerci: the apical part is on average rather short and the outer margin less concave than

Table 5. Mean body dimensions with standard deviations and ranges for 17 localities of *Ephippiger terrestris*. BW – Body weight, LB – length of body, LP – length of pronotum, LT – length of protibia, LF – length of hind femur.

No.	Locality	n	BW (g)	LB (mm)	LP (mm)	LT (mm)	F (mm)
1A.	Mézel	21	1.27 ± 0.13 1.1 – 1.5	28.0 ± 1.36 25 – 29	7.40 ± 0.42 6.8 – 8.7	7.75 ± 0.28 7.3 – 8.2	15.1 ± 0.55 14.1 – 16.5
2.	C. d. Maure	28	1.01 ± 0.13 0.7 – 1.2	25.8 ± 1.43 23 – 28	6.92 ± 0.24 6.4 – 7.3	7.32 ± 0.28 6.8 – 7.8	13.8 ± 0.47 13.2 – 15.1
3.	Gréolières	23	1.27 ± 0.18 0.8 – 1.6	26.8 ± 1.53 22 – 29	7.26 ± 0.41 6.4 – 8.0	7.51 ± 0.35 6.9 – 8.0	15.0 ± 0.60 13.4 – 16.0
4.	C. de Braus	20	1.82 ± 0.16 1.5 – 2.2	30.2 ± 0.87 29 – 35.5	7.93 ± 0.43 7.2 – 8.5	8.36 ± 0.26 7.8 – 8.8	16.3 ± 0.53 15.0 – 17.1
5.	C. de Castill.	20	2.56 ± 0.42 1.5 – 3.3	33.2 ± 1.64 31 – 37	8.79 ± 0.50 8.1 – 10.0	9.18 ± 0.40 8.2 – 9.7	17.9 ± 0.76 16.8 – 19.5
6.	Scravaion	20	1.34 ± 0.12 1.1 – 1.5	27.5 ± 1.23 26 – 30	7.59 ± 0.40 6.6 – 8.3	7.89 ± 0.38 6.9 – 8.3	15.1 ± 0.51 13.9 – 15.9
7A.	Tende	18	1.25 ± 0.12 1.0 – 1.5	26.6 ± 1.04 25 – 28	7.44 ± 0.40 6.8 – 8.2	7.76 ± 0.35 7.1 – 8.3	15.3 ± 0.71 14.6 – 16.2
8.	Vievola 1	21	1.04 ± 0.15 0.8 – 1.4	25.7 ± 0.86 24 – 28	7.19 ± 0.51 6.4 – 8.2	7.39 ± 0.32 6.8 – 7.9	14.4 ± 0.68 13.2 – 15.5
9.	Vievola 2	19	1.02 ± 0.10 0.8 – 1.2	25.5 ± 0.90 23 – 27	7.10 ± 0.26 6.6 – 7.6	7.39 ± 0.33 6.8 – 8.2	14.4 ± 0.45 13.4 – 15.1
10.	C. d. Tende 1	17	1.01 ± 0.13 0.7 – 1.2	24.7 ± 1.50 20 – 26	7.26 ± 0.43 6.6 – 8.1	7.25 ± 0.32 6.8 – 7.8	14.0 ± 0.62 13.1 – 15.1
11.	C. d. Tende 2	19	1.00 ± 0.10 0.8 – 1.2	24.0 ± 0.70 23 – 25	7.12 ± 0.28 6.7 – 7.6	7.01 ± 0.24 6.7 – 7.7	13.5 ± 0.59 11.9 – 14.2
12.	C. d. Tende 3	23	1.07 ± 0.09 0.9 – 1.2	24.9 ± 0.97 23 – 26	7.27 ± 0.47 6.1 – 8.1	7.13 ± 0.28 6.7 – 7.6	13.7 ± 0.57 12.8 – 15.3
13.	Vall. d. Arma	24	1.01 ± 0.09 0.8 – 1.2	25.0 ± 0.86 23 – 27	6.81 ± 0.39 6.3 – 7.7	6.97 ± 0.24 6.7 – 7.4	13.4 ± 0.45 12.0 – 14.4
14A.	Naggio	23	0.79 ± 0.10 0.7 – 1.0	23.7 ± 1.11 20 – 25	6.40 ± 0.12 6.2 – 6.6	6.85 ± 0.18 6.6 – 7.2	13.0 ± 0.44 12.2 – 14.1
15.	Mt. Grona	17	0.89 ± 0.11 0.7 – 1.1	24.3 ± 1.18 23 – 27	7.15 ± 0.43 6.4 – 8.0	7.07 ± 0.41 5.9 – 7.7	13.4 ± 0.58 12.4 – 14.2
17.	Collobr.	17	2.42 ± 0.26 2.1 – 3.0	32.1 ± 1.73 29 – 36	8.84 ± 0.53 8.0 – 9.3	9.72 ± 0.46 8.9 – 10.5	18.8 ± 0.75 18.0 – 20.4
18.	Fayence	25	2.41 ± 0.28 1.8 – 3.1	33.0 ± 1.37 30 – 36	8.27 ± 0.48 7.6 – 9.5	9.41 ± 0.46 8.8 – 10.6	18.5 ± 0.77 16.6 – 19.8

Table 6. Interrelations between mean body dimensions of *Ephippiger terrestris* (17 localities).

	regression	correlation
body weight/body length	LB = 0.18 BW – 3.45	r = 0.98
pronotum length/body length	LB = 0.18 LP × 2.22	r = 0.93
tibia length/femur length	LF = 0.49 LT + 0.45	r = 0.99
pronotum length/femur length	LF = 0.34 LP + 2.29	r = 0.95

Table 7. Relations between mean body dimensions (table 5) and altitude (H in km) for *Ephippiger terrestris* (17 localities).

	regression	correlation
body weight/altitude	$BW = -1.04 H + 2.4$	$r = -0.75$
body length/altitude	$LB = -5.74 H + 33.0$	$r = -0.74$
pronotum length/altitude	$LP = -1.11 H + 8.6$	$r = -0.69$
tibia length/altitude	$LT = -1.79 H + 9.6$	$r = -0.83$
femur length/altitude	$LF = -3.65 H + 18.8$	$r = -0.82$

Table 8. Ratios between some measures of the epiproct (cf. Fig. 3A) in *Ephippiger terrestris*.

No.	Locality	n	EB/EA	EA/EC	EL/EM
1B.	Mézel	21	0.82 ± 0.08	1.26 ± 0.12	1.29 ± 0.20
2.	C. d. Maure	28	0.83 ± 0.09	1.25 ± 0.09	1.10 ± 0.10
3.	Gréolières	23	0.77 ± 0.05	1.34 ± 0.13	1.06 ± 0.13
4.	C. d. Braus	20	1.08 ± 0.09	0.98 ± 0.07	1.02 ± 0.15
5.	C. d. Castell.	20	1.15 ± 0.11	0.96 ± 0.07	0.94 ± 0.10
6.	Scravaion	20	1.25 ± 0.13	0.86 ± 0.07	0.82 ± 0.10
7.	Tende	18	1.13 ± 0.11	0.92 ± 0.08	0.95 ± 0.09
8.	Vievola 1	21	1.14 ± 0.17	0.94 ± 0.10	0.88 ± 0.06
9.	Vievola 2	19	1.10 ± 0.14	0.98 ± 0.09	0.88 ± 0.06
10.	C. d. Tende 1	17	0.97 ± 0.13	1.10 ± 0.13	0.84 ± 0.12
11.	C. d. Tende 2	19	0.96 ± 0.10	1.15 ± 0.09	0.84 ± 0.10
12.	C. d. Tende 3	23	0.99 ± 0.13	1.12 ± 0.07	0.83 ± 0.09
13.	Vall. d. Arma	24	0.93 ± 0.13	1.19 ± 0.13	0.74 ± 0.11
14A.	Naggio	23	0.82 ± 0.08	1.25 ± 0.06	0.78 ± 0.05
15.	Mt. Grona	20	0.86 ± 0.05	1.22 ± 0.05	0.79 ± 0.07
17.	Collobr.	17	0.97 ± 0.10	1.13 ± 0.09	1.21 ± 0.09
18.	Fayence	25	0.99 ± 0.10	1.09 ± 0.08	1.11 ± 0.09

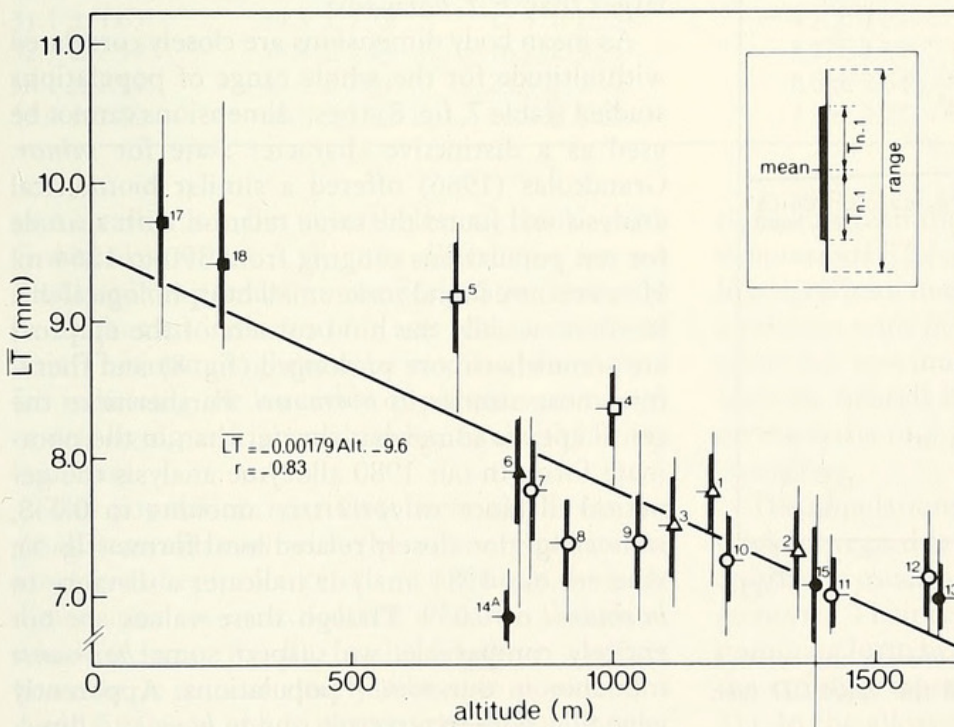


Fig. 8. The relation between mean length of tibia (LT) and altitude (H) in *Ephippiger terrestris*.

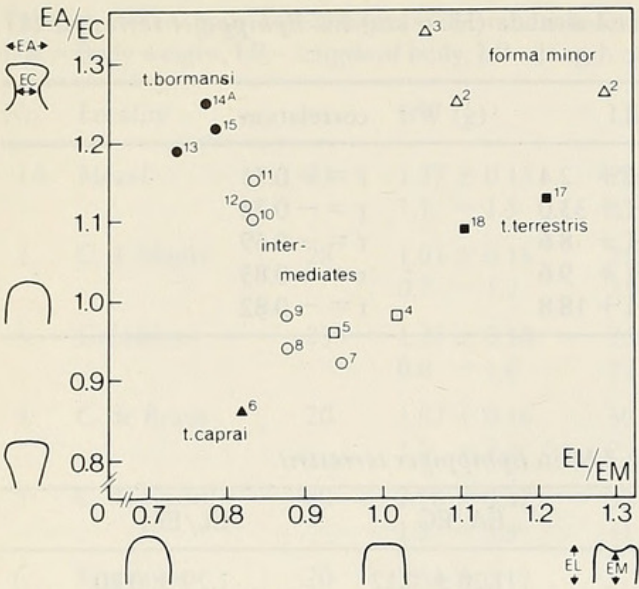


Fig. 9. The form of the epiproct in *Ephippiger terrestris*: relation between the ratios EA/EC and EL/EM (see text).

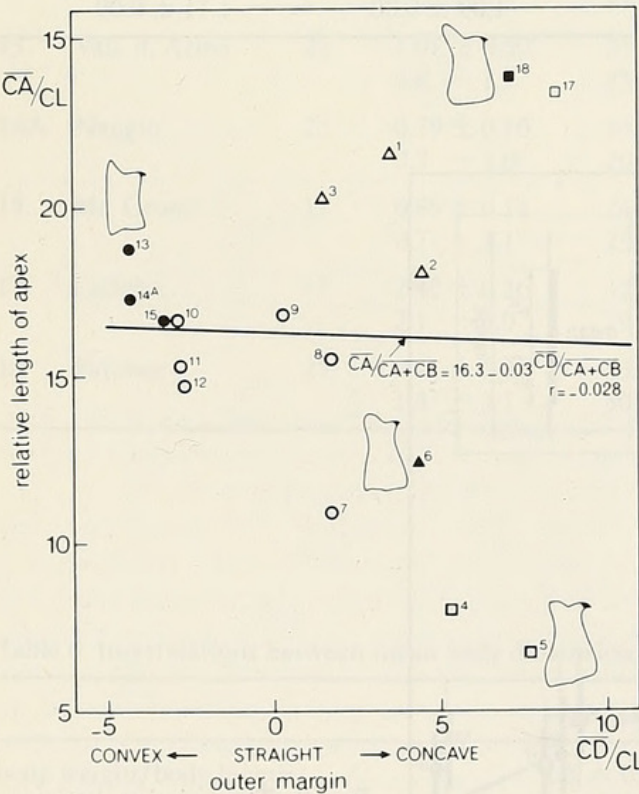


Fig. 10. Diagram of the relation between the relative length of the cercal apex (CA) and the value CD (see text).

in the nominate form. Furthermore, we confirm Nadig's description of the granular campus medianus and the receding fastigium verticis in *caprai*. Our allozyme analysis showed an evidently distinct position of *caprai* with a genetical distance $D = 0.068$ for *E. t. terrestris* and $D = 0.076$ for *E. t. bormansi*. Such distances are rather low, but still in the normal range for subspecies, for which Menken & Ulenberg (1987) give a general range of 0.02-0.22.

Our study of three populations of *E. t. bormansi* confirmed Nadig's (1980) observations. The animals were generally very small and the abdomen is often marked with three rows of dark spots and a lateral yellow band. The epiproct has in the average rather small, laterally protruding, hind corners. The cerci have a short apex with a straight or even slightly convex outer margin. The basal part of the cerci tapers only slightly towards the apex; this character corresponds with Nadig's not or hardly thickened cercal base. The apical part of the titillator is slender. The campus medianus is smooth and the fastigium verticis steep. In our allozyme analysis the distance to the *E. t. terrestris* populations is rather small: $D = 0.0439$, but this is probably an underestimation because we did not determine the distance to the populations no. 17 and/or 18 that were unfortunately not included in the 1981 series.

The *forma minor* is obviously characterized by small body dimensions. We consider our samples 1 and 2 as typical. Table 5 and fig. 7 show that these samples are in the mean much smaller than the other *E. t. terrestris* populations, but somewhat larger than *E. t. bormansi*.

As mean body dimensions are closely correlated with altitude for the whole range of populations studied (table 7, fig. 8) these dimensions cannot be used as a distinctive character state for *minor*. Grandcolas (1986) offered a similar biometrical analysis and found the same relation with altitude for ten populations ranging from 390 to 1264 m. However, we found some small morphological differences: usually the hind corners of the epiproct are somewhat more prolonged (fig. 8) and therefore more similar to *bormansi*. Furthermore the cercal apex is somewhat shorter than in the nominate form. In our 1980 allozyme analysis the genetical distance to *terrestris* amounts to 0.048, rather high for closely related local forms (fig. 5), whereas our 1981 analysis indicates a distance to *bormansi* of 0.039. Though these values are not entirely comparable, we suspect some *bormansi* influence in our *minor* populations. Apparently gene flow both in *terrestris* and in *bormansi* direc-

Table 9. Mean dimensions of the cerci of *Ephippiger terrestris*, cf. Fig. 3B (one unit = 1/40 th mm).

No.	Locality	n	CA	CB	CD	CL
1B.	Mézel	21	14.5 ± 3.75	52.6 ± 4.22	2.40 ± 1.85	67.1 ± 4.00
2.	Col de Maure	29	11.2 ± 3.12	50.3 ± 4.37	2.83 ± 1.26	61.5 ± 5.74
3.	Gréolières	23	13.9 ± 2.62	54.6 ± 4.02	0.85 ± 1.31	68.4 ± 4.28
4.	Col de Braus	20	5.7 ± 2.54	65.2 ± 3.04	3.75 ± 2.42	70.8 ± 3.53
5.	C. d. Castillon	20	5.0 ± 3.05	69.7 ± 4.10	5.52 ± 1.79	74.9 ± 4.79
6.	C. Scravaion	20	8.3 ± 2.66	58.5 ± 3.20	2.90 ± 1.42	66.9 ± 3.20
7.	Tende	29	7.0 ± 3.41	56.1 ± 2.34	1.12 ± 1.65	63.1 ± 5.04
8.	Vievolà 1	19	10.6 ± 2.93	53.7 ± 4.12	1.16 ± 1.63	64.3 ± 3.63
9.	Vievolà 2	19	11.1 ± 2.62	55.2 ± 4.34	0.24 ± 1.29	66.1 ± 4.59
10.	C. d. Tende 1	17	12.4 ± 3.57	61.6 ± 3.44	− 2.06 ± 1.21	74.1 ± 3.86
11A.	C. d. Tende 2	20	11.0 ± 3.21	60.4 ± 3.23	− 1.92 ± 1.53	71.4 ± 3.53
12.	C. d. Tende 3	23	10.5 ± 3.13	60.8 ± 4.83	− 1.85 ± 1.22	71.3 ± 4.29
13.	Vall. del Arma	25	13.8 ± 3.11	66.2 ± 6.22	− 2.90 ± 1.01	74.0 ± 4.50
14A.	Naggio	23	11.6 ± 1.69	55.6 ± 2.67	− 2.83 ± 1.14	67.3 ± 3.63
15.	Mt. Grona	20	12.2 ± 3.01	60.5 ± 3.89	− 2.35 ± 0.99	72.7 ± 5.77
17.	Collobr.	17	18.2 ± 2.75	58.5 ± 4.80	6.70 ± 2.17	76.7 ± 4.28
18.	Fayence	25	18.2 ± 4.20	58.5 ± 5.55	5.60 ± 1.87	76.7 ± 5.19

CF	CE	CA / CL × 100	CD / CL × 100	CF / CE × 100	No.
32.8 ± 1.80	41.3 ± 2.57	21.5 ± 5.31	3.6 ± 2.74	79.6 ± 6.12	1B.
32.7 ± 1.75	40.9 ± 2.41	18.0 ± 4.36	4.5 ± 2.21	80.2 ± 4.50	2.
32.9 ± 2.11	41.0 ± 2.84	20.2 ± 3.52	1.3 ± 1.90	80.6 ± 4.65	3.
28.5 ± 2.37	45.2 ± 2.49	8.0 ± 3.46	5.3 ± 3.50	63.3 ± 6.06	4.
30.8 ± 2.48	49.2 ± 2.27	6.7 ± 3.92	7.7 ± 2.68	62.6 ± 4.50	5.
29.2 ± 1.48	41.3 ± 2.13	12.4 ± 3.70	4.4 ± 2.16	70.9 ± 4.31	6.
29.6 ± 1.81	41.1 ± 3.15	10.9 ± 4.51	1.8 ± 2.58	71.9 ± 4.62	7.
29.4 ± 2.41	41.2 ± 1.63	15.5 ± 5.41	1.8 ± 2.47	71.5 ± 4.43	8.
29.4 ± 1.64	40.1 ± 3.07	16.8 ± 3.75	0.4 ± 1.94	73.6 ± 4.20	9.
32.3 ± 2.20	41.2 ± 3.07	16.6 ± 4.45	− 2.8 ± 1.56	78.9 ± 5.63	10.
32.5 ± 1.76	40.1 ± 2.76	15.3 ± 4.16	− 2.7 ± 2.14	81.3 ± 5.49	11A.
32.9 ± 1.82	40.5 ± 2.25	14.7 ± 4.28	− 2.6 ± 1.74	80.6 ± 5.25	12.
32.1 ± 2.02	39.1 ± 3.60	18.8 ± 4.23	− 4.2 ± 1.50	82.7 ± 8.59	13.
31.1 ± 1.65	34.3 ± 1.79	17.3 ± 1.93	− 4.2 ± 1.71	91.5 ± 6.40	14A.
32.9 ± 2.57	38.8 ± 2.43	16.7 ± 3.25	− 3.2 ± 1.34	84.7 ± 5.36	15.
38.1 ± 2.54	49.8 ± 2.81	23.3 ± 4.38	8.6 ± 2.64	76.5 ± 4.70	17.
35.0 ± 2.59	48.7 ± 3.82	23.8 ± 5.10	7.3 ± 2.27	72.1 ± 6.34	18.

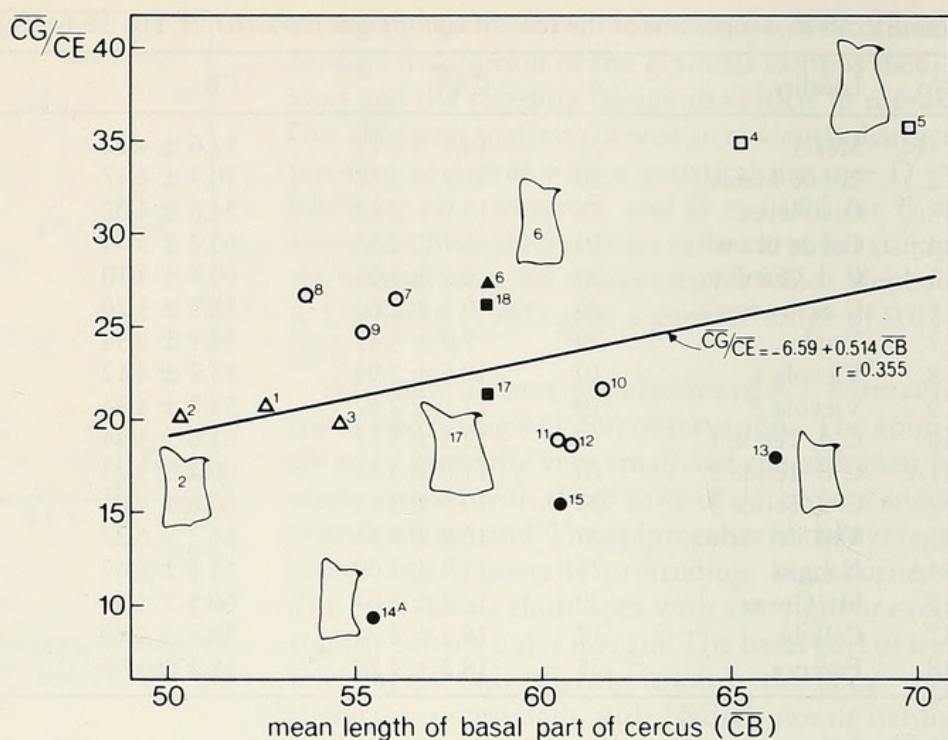
tion is rather low, but nevertheless we think – with Grandcolas (1986) – that the differences are too small and too gradual for the designation *minor* to be used as an indication for any real taxonomical unit. This term might only be used as a short-hand for indicating the assembly of populations of *terrestris* living at higher altitudes, but without any boundary.

The population near Gréolières (3) has many small resemblances with the *minor* populations, viz. form of epiproct, cerci and titillators. Its body dimensions are in accordance with the altitude at which it lives (fig. 8). In the allozyme analysis, however, it is more closely related to populations 4 and 5 (figs. 4 and 5) than to the *minor* popula-

tions, to which the genetic distance is the same as to *bormansi*. The occurrence of dark spot markings in a significant number of individuals also indicates a relation with *bormansi*. Nadig (1980) incorporated his specimens from Gréolières (Cheiron) with the hybrids between *terrestris* and *bormansi* on the basis of a great number of morphological characters.

The populations 4 and 5 also offer some difficulties with regard to their position. The form of their epiproct is usually intermediate between *caprai* and *terrestris*. Their cerci differ conspicuously from the nominate form by the very short apex (fig. 10) and the strongly tapering form of the basal part (fig. 11). In the allozyme analysis their distance to po-

Fig. 11. Relative measure of tapering of the basal part of the cercus.



pulation 3 is small (fig. 5), much smaller than to the populations 6 and 7. Population no. 5 is judged by Nadig (l.c.) as belonging to the nominate form. We add the remark that these populations show some differences with the more western populations from the *terra typica* and exhibit probably some influence from *caprai*.

One of the aims of this study was to investigate the populations along the Tende transect (sites 7-12). Nadig (1980) collected specimens from the Col de Tende which he judged to be hybrids between the subspecies *terrestris* and *bormansi*. Our allozyme analysis shows all six populations along the transect to be closely related (figs. 4 and 5). The distances of this group to *caprai* and *terrestris* are of the same order, those to *bormansi* are smaller. In concordance with the geographical situation the sites 7-9 form one subgroup and the sites at the south side of the Col de Tende (10-12) another one, the genetic distance of the latter group to *bormansi* being significantly smaller. The form of the epi-proct is intermediate between *bormansi*, *terrestris* and *caprai* with the sites 7-9 closest to *caprai* and the sites 10-12 closest to *bormansi*. In the form of the cerci *bormansi* influences are generally evident, but site 7 approaches *caprai*. With regard to the slenderness of the apical part of the titillators a gradient between *caprai* and *bormansi* was found especially at the sites 7-9. The populations resembled the *bormansi* character state. However, this also appears to prevail in the *minor* populations. Nadig (l.c., fig. 36) showed the existence of a continuous transition in slenderness from the *caprai*- towards the *bormansi*-state with the *terres-*

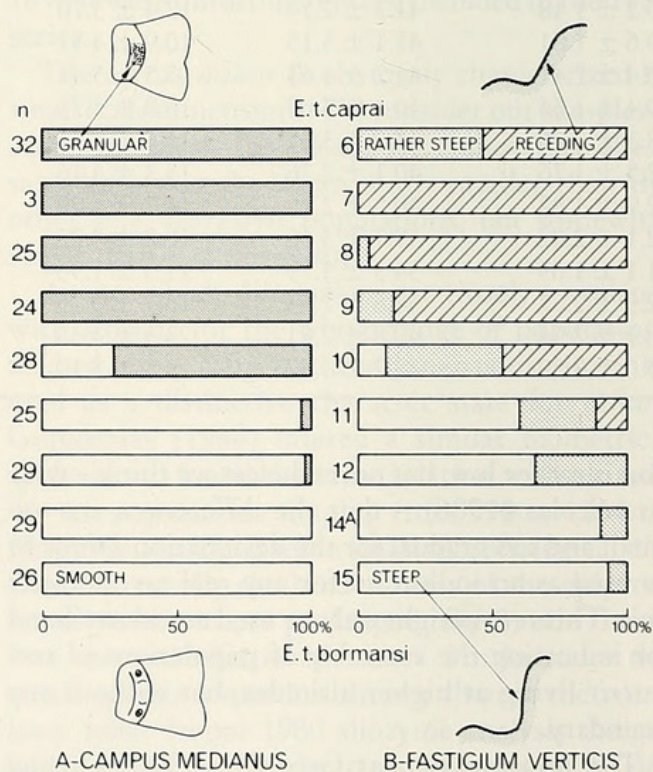


Fig. 12. A (left): Distribution of the character states granular and smooth of the campus medianus on the pronotum in *Ephippiger terrestris* along the Tende transect. B (right): Distribution of the character states steep - rather steep - receding of the fastigium verticis of the head of *E. terrestris*.

Table 10. The ratio TL/TA as a measure of the slenderness of titillators in *Ephippiger terrestris*.

No.	Location	n	TL/TA
2.	Col de Maure	30	10.9 ± 1.22
3.	Gréolières	21	11.0 ± 1.88
6.	Scravaion	10	5.8 ± 0.61
7.	Tende	20	6.4 ± 0.83
8.	Vievol 1	20	6.9 ± 1.03
9.	Vievol 2	14	8.1 ± 1.35
10.	C. d. Tende 1	10	10.7 ± 1.26
11A.	C. d. Tende 2	7	11.0 ± 1.73
12.	C. d. Tende 3	5	10.7 ± 2.24
13.	Vall. d. Arma	21	12.2 ± 2.40
14A.	Naggio	19	10.5 ± 1.25
15.	Mt. Grona	19	11.8 ± 1.18

tris form at an intermediate and overlapping position. However, he did not relate these data to geographical positions.

At sites 7-9 the campus medianus is granular, as in *caprai*. At the sites along the Col de Tende this state changes towards the smooth condition characteristic for *bormansi*. A gradual transition is also found with regard to the fastigium verticis: reced-

ing in *caprai* and predominantly receding at sites 7-9, with a gradual transition along the Col de Tende sites towards the steep condition in *bormansi*.

With regard to the colour of the abdomen a gradient was established in the occurrence of (plain)-green and the abdominal marking with rows of black spots.

Where Nadig (1980) doubted if *caprai* was involved in the origin of the intermediate populations and thought the mountain ridge forms a sharp boundary for *caprai*, we think we have sufficient evidence suggesting *caprai* influences existing in the region of intermediate populations, especially in the neighbourhood of Tende (where the colour of the abdomen also resembles *caprai*), but perhaps also in a wider area (viz. site 5).

The *bormansi* influence is quite clear at the Col de Tende sites, but is – according to Nadig – much more widespread. It is probable that this influence is also present in the *minor* areas and is responsible for the finding of supposed *bormansi* specimens as mentioned in literature (viz. at the Col de la Cine).

Summarizing: it is fruitfull to consider *Ephippiger terrestris* – with Nadig – as a species occupying an extensive area in SE France and N. Italy.

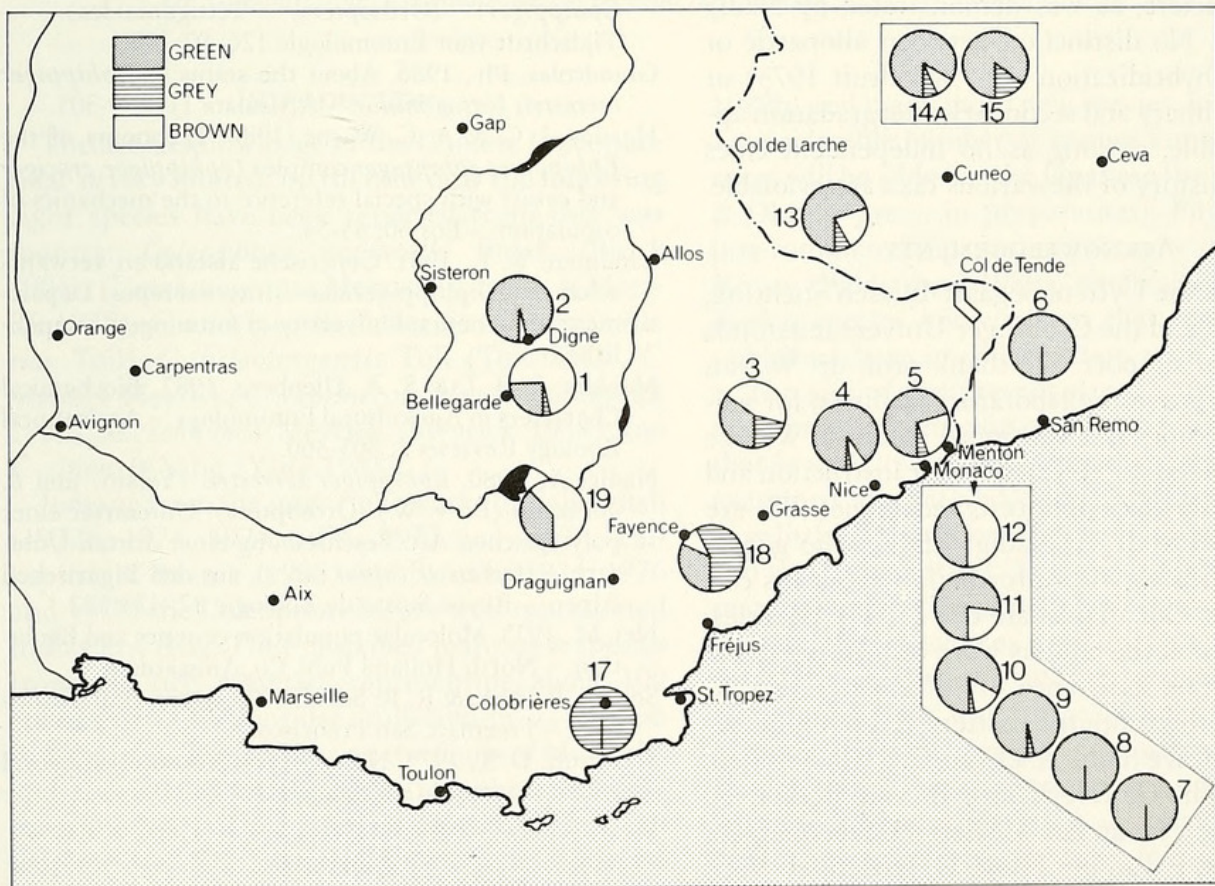
Fig. 13. The colour of the abdomen in *Ephippiger terrestris*.

Table 11. Colour and abdomen marking in *Ephippiger terrestris* (percentages).

No.	Locality	n	light green	plain green	dark green	greyish green	grey	brown	rows of dark spots
6.	Scravaion	32	—	100	—	—	—	—	—
7.	Tende	25	5	93	—	3	—	—	—
8.	Vievola 1	25	—	72	4	24	—	—	—
9.	Vievola 2	24	4	92	—	—	4	—	—
10.	C. d. Tende 1	28	—	64	4	15	4	15	11
11A.	C. d. Tende 2	25	4	64	—	8	—	24	29
12.	C. d. Tende 3	29	—	31	—	14	—	55	49
13.	Vall. d. Arma	41	3	40	—	12	8	23	—
14A.	Naggio	29	4	21	—	48	7	11	52
15.	Mt. Grona	26	12	35	—	39	16	—	—

It is possible to distinguish the three subspecies *terrestris*, *caprai* and *bormansi*, but only at the outer margins of this area. All local populations exhibit great variability in their characters, so that it is often impossible to identify individuals to their subspecies. No clear boundaries nor narrow hybridisation zones exist between the subspecies, but there is a large transitional field: in the centre of the distribution area lies a quadrangular area (approximately 50 x 70 km) with intermediate populations, containing characters of all three subspecies. Their influences manifest themselves often in clinal characters, as was demonstrated by Nadig and herein. No distinction between allopatric or parapatric hybridization (e.g. Woodruff 1973) or between primary and secondary intergradation appears possible, as long as no independent clues about the history of the various taxa are available.

ACKNOWLEDGEMENTS

We thank the Uyttenboogaart-Eliassen Stichting, Amsterdam and the Groninger Universiteitsfonds for financial support. We thank prof. dr. W. van Delden for providing laboratory facilities, for valuable discussion and continued interest. We are also indebted to dr. H. van Dijk for instruction and help with the electrophoresis techniques. We are very grateful to dr. A. Nadig (Chur), who generously supplied us with information about his collecting sites. Our thanks are due to H. J. de Vries, who undertook the tedious work of measuring the epiprocts. The assistance of M. Zijlstra and K. Vrieling with computer matters is gratefully acknowledged. We thank A. Decae, G. J. van Klinken, H. Hiddingh, G. Overkamp, B. van Berkel, R. Schoenmaker, J. van der Meulen, H. Steenbergen, K. van Dijk, P. van der Hurk, H. Jansen, H. Vondeling, B. Kruijt and L. Tromp for assistance in collecting the insects. We are grateful to Dr. M. G.

Ritchie for critically reading the manuscript and for correcting the English. Furthermore we thank Mrs. J. Poelstra for typing the manuscript and D. Visser and D. van der Spek for making the drawings.

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Received: 4 January 1989

Revised version accepted: 29 May 1989



Landman, W, Oudman, L, and Duijm, M. 1989. "Allozymic and morphological variation in *Ephippiger terrestris* (Yersin, 1854) (Insecta, Orthoptera, Tettigoniioidea)." *Tijdschrift voor entomologie* 132, 183–198.

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