

# Analysis of the geographical variation of elytral color polymorphisms in three species of soldier beetles, *Chauliognathus* Hentz (Cantharidae) in southern Brazil

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**ABSTRACT.** In the present report, we investigate polymorphism in three of the Brazilian species of *Chauliognathus* Hentz, 1930 (Coleoptera, Cantharidae), by analyzing the geographical color pattern variation of the elytra in *C. flavipes*, *C. fallax* and *C. octomaculatus*. These species belong to the mullerian complex called the “yellow-black”. They are usually found in clusters on their host plants at various locations and present similarities in the external body morphology and in the color pattern of the elytra and the pronotum. *Chauliognathus flavipes* is the most common species with eight phenotypic classes followed by *C. fallax* and *C. octomaculatus* with six and two phenotypic classes respectively. The analyses indicate a statistically significant difference in the frequencies of colour patterns of the three species over the entire area sampled. In general, the significant differences were observed between the regions of the State of Rio Grande do Sul ( $p < 0.05$ ) but were not found within the individual regions except in the case of the Metropolitan region. That region and its three microregions demonstrated a positive co-relationship between an increase in altitude and the occurrence of diversity in *C. flavipes* and *C. fallax* ( $r = 0.860$ ,  $p < 0.01$ ;  $r = 0.974$ ,  $p < 0.01$ , respectively).

**KEY WORDS.** Coleoptera; mullerian mimicry; aposematism.

**RESUMO. Análise da variação geográfica no polimorfismo de coloração dos élitros em três espécies de *Chauliognathus*, Hentz (Cantharidae) no Sul do Brasil.** No presente estudo investigamos o polimorfismo em três espécies de *Chauliognathus* Hentz, 1930 (Coleoptera, Cantharidae), analisando a variação geográfica no padrão de coloração dos élitros em *C. flavipes*, *C. fallax* e *C. octomaculatus*. Estas espécies pertencem ao complexo mülleriano chamado “amarelo-preto”. São encontradas formando grandes agregados sobre as plantas que utilizam como substratos de alimentação e apresentam semelhança morfológica e para a coloração dos élitros e pronoto. *Chauliognathus flavipes* é a espécie mais freqüente e apresenta o maior número de padrões fenotípicos (8) seguidos de *C. fallax* e *C. octomaculatus* com seis e dois padrões respectivamente. Diferenças significativas nas freqüências dos padrões de coloração nas três espécies foram detectadas ao longo da área analisada. Em geral, as diferenças foram observadas entre as regiões do Estado do Rio Grande do Sul ( $p < 0,05$ ), mas não dentro das regiões, exceto para a região Metropolitana. Nas três microregiões que formam a região Metropolitana encontrou-se uma correlação positiva entre o aumento da altitude e a diversidade em *C. flavipes* e *C. fallax* ( $r = 0,860$ ,  $p < 0,01$ ;  $r = 0,974$ ,  $p < 0,01$ , respectivamente).

**PALAVRAS-CHAVE.** Coleoptera; mimetismo mülleriano; aposematismo.

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Species that exhibit visible polymorphisms are ideal for studying the micro-evolutionary forces that maintain genetic variation in nature. The colour is one of the few phenotypic characters that vary in discrete classes, and this suggests a character with a simple genetic base that is thus easily applied in classical genetic work (see for example, EKENDALL & JOHANNESSON 1997, HOFFMAN & BLOUIN 2000), and classical studies with *Biston betularia* Linnaeus, 1758 (KETTLWELL 1961) and *Cepaea* sp. (JONES *et al.* 1977).

A fuller understanding of how colour polymorphisms in natural populations are maintained is fundamental in evolutionary biology. Considerable indirect evidence and some concrete proof indicates that the variation may be sustained through selective predation by hunting predators who use colour vision to locate their prey (SILLÉN-TULBERG & BRYANT 1983, ENDLER 1988, WHITELEY & OWEN 1997, MALLET & JORON 1999).

The existence of color polymorphisms and the factors

that maintain this polymorphism in Müllerian mimetic organisms have generated much debate and renewed the interest in mimicry (MACDOUGALL & DAWKINS 1998, JORON & MALLET 1998, MALLET & JORON 1999, JORON 2005). In this kind of mimetism, the monomorphism is thought to evolve due to stabilization selection on the color pattern on aposematic species.

Many coleopteran species exhibit striking elytra colour polymorphisms and so provide an excellent system to study questions about the evolution and maintenance of polymorphisms (KEARNS *et al.* 1990, BERNSTEIN & BERNSTEIN 1998, MACHADO & ARAÚJO 1999, MACHADO *et al.* 2004).

The genus *Chauliognathus* Hentz, 1930 occurs in Australia, South and North America and runs to more than 250 species, most of them occurring in Neotropical regions. Despite its diversity and ready availability for sampling, there are few studies about the biology of these species. In Brazil, DELKESKAMP (1939) described nearly 100 species that can be collected between October and March (Spring and Autumn in the Southern Hemisphere).

In the present report, we investigate the geographical variation in the frequencies of the coloration patterns by analysing the colour pattern variation of the elytra in three Brazilian species to improve our understanding of the evolutionary dynamics of colour polymorphisms in the *Chauliognathus* beetle. The species analysed are part of the "yellow-black" complex described by MACHADO *et al.* (2001). They present similarities in the external body morphology and in the colour pattern of the elytra and the pronotum. They are usually found in clusters on their host plants at various locations in the southern regions of Brazil. The study of the occurrence and maintenance of the variations of colour patterns in *Chauliognathus* is an alternative approach to the models used in similar investigations of butterfly species (MACHADO *et al.* 2004). In both cases, the objective is a better understanding of the mechanisms involved in the evolution of the polymorphism of Müllerian mimicry.

## MATERIAL AND METHODS

### Samples

Adult insects were collected by hand from the plants at the feeding sites located in the state of Rio Grande do Sul (the most southerly state of Brazil). The sampling localities, geographical coordinates and the number of specimens are presented in table I for *C. flavipes* Fabricius, 1781, table II for *Chauliognathus fallax* Germar, 1824 and table III for *C. octomaculatus* Pic, 1915. The specimens were collected between October 1998 and March 2002. The feeding plants in most of the locations were *Eryngium* sp. (Tourn.) Linnaeus (Apiaceae) although in a few places *Escallonia* sp. Mutis ex Linnaeus f. (Grossulariaceae) and *Eucalyptus* sp. L' Her. (Myrtaceae) were also present.

The colour patterns were defined as a function of the presence or absence of black spots, and by the size of the spots. The spots sometimes appear as strips, and some individuals show no spots at all or are of a very dark colour. There are also

variations in the width and shape of the strips. The main colours of these species are illustrated in figure 1. A reference sample of all the phenotypes found was deposited in the Cantharidae Collection, Molecular Genetic Laboratory, Universidade do Vale do Rio dos Sinos.

### Data analysis

The Shannon-Weaver index (PIELOU 1977) was used to compare the overall colour variation (phenotypic diversity) among the samples. A high index indicated a highly variable sample, that is, that most of the colour morphs were present in that sample. We compared the actual diversity value to the maximum possible diversity by using the evenness index ( $J'$ ), according to PIELOU (1977). Evenness is greatest when morphs species are equally abundant. The dominance index ( $D$ ) (SIMPSON 1949), showed the influence of patterns which appeared with greater frequency in the phenotypic diversity.

We used cluster analysis to group the samples. First, we calculated the Manhattan-distances and the results were used to construct the dendrogram by the unweighted pair-group method with arithmetic mean (UPGMA). The  $\chi^2$ , or exact permutation test (ROLF & BENTZEN 1989) with 1000 randomizations was employed to evaluate the statistical significance of the differences observed in the frequencies of elytra color patterns among the sample groups. This test is useful when the expected values are very small, as is the case of some morphs. The frequency of the morphs for each species was compared within and among different geographic regions in Rio Grande do Sul as shown in figure 2.

In each of the regions, different samples were obtained representing the different microregions. Where the frequencies of the patterns were not significantly different one from the other, the microregions were grouped as representatives of the entire region, otherwise they were analyzed separately.

## RESULTS

The analysis of the geographical variation of the polymorphisms of the elytra in *C. flavipes*, *C. fallax* e *C. octomaculatus*, showed that there were statistically significant differences in the frequencies of colour patterns of the three species over the entire area sampled. In general, the significant differences were observed between the regions of the State of Rio Grande do Sul ( $p < 0.05$ ) but were not found within each region except in the case of the Metropolitan region (Fig. 2).

Table I shows the frequencies of the eight morphs found in *C. flavipes* collected in fifteen populations from six regions of the Rio Grande do Sul state. In all the samples, the morph 4 were the most common but showed a wide range in frequency between 24.8% (Northwest) and approximately 40% (Metropolitan) (Tab. I). The variation of the morphs 2 and 3 ranged from 12 to 15%, except in the sample from Northeast region where the frequency was lower (7%). On the other hand, the morphs 6 and 8 were rare in all populations and had the lowest frequencies (Tab. I).

Species	Morphs								Elytra colour Yellow-black
	1	2	3	4	5	6	7	8	
(1) <i>C. flavipes</i>									
(2) <i>C. fallax</i>									
(3) <i>C. octomaculatus</i>									

Figure 1. Pattern of variation in elytral color for species of *Chauliognathus*. (1) *Chauliognathus flavipes*, (2) *C. fallax*, (3) *C. octomaculatus*.

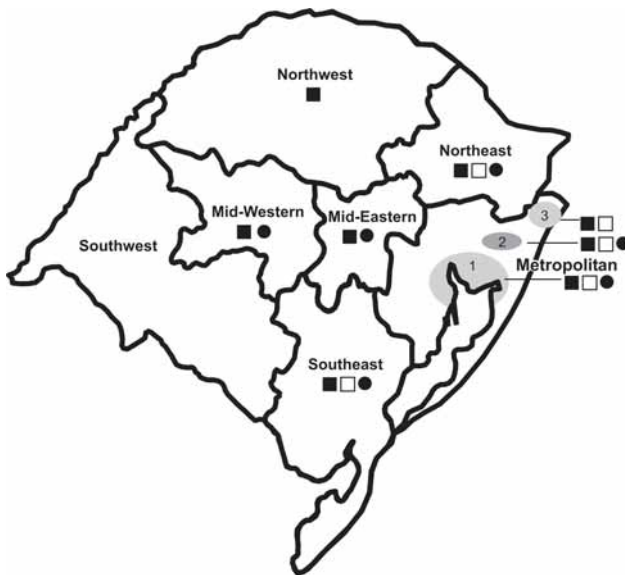


Figure 2. Geographic locations of the sampled populations of genus *Chauliognathus* in Rio Grande do Sul state (Brazil). (■) *C. flavipes*; (□) *C. fallax*; (●) *C. octomaculatus*. Metropolitan 1, 2 and 3 correspond to the micro regions Porto Alegre, Gramado/Canela and Osório, respectively.

The Metropolitan region presents statistically significant internal differences ( $p < 0.05$ ) – especially between the Porto Alegre/Gramado-Canela (group A, Fig. 3) as compared to the Osório (group B). The greatest difference in the frequency of colour patterns found between the samples was that between

the Northwestern and Northeastern regions (10.6%) whilst the smallest was that separating those from Porto Alegre and Gramado/Canela (1.8%) – herein denominated *Metropolitan 1* and 2 (Fig. 2). In the centre of the State, the Mid-Western and Mid-Eastern regions did not present significant differences in the frequencies of the coloration patterns detected and are therefore grouped in one single cluster (C).

The quantitative description of the polymorphism was obtained from the Shannon-Weaver ( $H'$ ) and the homogeneity index ( $J$ ) and indicated a similar degree of diversity (polymorphism) in all of the populations. Notwithstanding this homogeneity, there are significant differences ( $\chi^2 116.98$ ;  $p < 0.000$ ) in the way in which the frequencies of the coloration patterns are distributed between the six regions, except in the case of the Mid-Western and Mid-Eastern regions ( $p > 0.05$ ) that make up the group C (Fig. 3).

The coloration polymorphism was analyzed in 1445 individuals in nine populations of *Chauliognathus fallax*, drawn from three regions (Fig. 2). Six patterns were found where the morph 3 presented frequencies above 50% – running from 52% in the Gramado/Canela microregion to 74% in the Osório microregion. Amongst the other morphs, only morph 4 appeared with a frequency above 10% and this one showed variation between 10% (Osório microregion) and 28% (Gramado/Canela microregion). Morph 6 had low frequency (0.23%) and then only in the Southeast region sample.

The analysis of the geographic variation of the coloration patterns suggests the formation of three clusters for this species (Fig. 4). The first cluster is made up of Porto Alegre, (*Metropolitan 1* in figure 2), Gramado/Canela (*Metropolitan 2* in figure 2) and the Southwest region; the second cluster by samples found on

Table I. Number, frequency and diversity index of elytra color patterns of *Chauliognathus flavipes* in samples sites.

Region	Altitude	Latitude (a)	Longitude	Elytra color patterns								Total	H'	J'	D	
	Mean ± SD	Lower - Higher	Lower - Higher	1	2	3	4	5	6	7	8					
Metropolitan																
Porto Alegre	40.2±19.9	29°40'S-30°06'S	50°46'W-51°19'W	0.1044	0.2045	0.1591	0.3808	0.0900	0.0108	0.0338	0.0166	1389	2.41	0.802	0.233	
Gramado/Canela	72.5±77.1	29°34'S-29°35'S	50°47'W-51°08'W	0.0951	0.1656	0.1442	0.4049	0.0982	0.0123	0.0706	0.0092	326	2.42	0.807	0.236	
Osório	16 (b)	29°18'S	49°41'W	0.0720	0.1360	0.1760	0.4320	0.0640	0.0000	0.1120	0.0080	125	2.29	0.764	0.258	
Northeast	817 b	29°10'S	51°10'W	0.0415	0.2490	0.0747	0.4938	0.0415	0.0041	0.0954	0.0000	241	2.02	0.673	0.324	
Northwest	414±163.9	28°22'S-29°17'S	51°30'W-54°08'W	0.1741	0.1135	0.3140	0.2480	0.0765	0.0211	0.0528	0.0000	379	2.44	0.815	0.212	
Mid-Western	91±53.7	29°34'S-29°41'S	53°26'W-54°40'W	0.1663	0.2386	0.1687	0.3470	0.0337	0.0072	0.0386	0.0000	415	2.28	0.761	0.236	
Mid-Eastern	68 (b)	29°42'S	52°30'W	0.1561	0.2543	0.1329	0.3353	0.0289	0.0160	0.0694	0.0116	173	2.40	0.800	0.225	
Southeast	19 (b)	31°21'S	51°58'W	0.1522	0.2536	0.1268	0.3551	0.0761	0.0000	0.0362	0.0000	276	2.28	0.760	0.237	
			Mean	0.1202	0.2019	0.1621	0.3746	0.0636	0.0084	0.0636	0.0057	3324	2.32	0.773	0.245	
			± SD	0.0489	0.0567	0.0691	0.0729	0.0262	0.0071	0.0288	0.0066		0.14	0.046	0.034	

(a) Latitude and longitude of the sampling places inside of the regions, (b) only one place sampling, (H') Shannon-weaver (J') Index Evenness, (D) dominance index.

Table II. Number, frequency and diversity index of elytra color patterns of *Chauliognathus fallax* in samples sites.

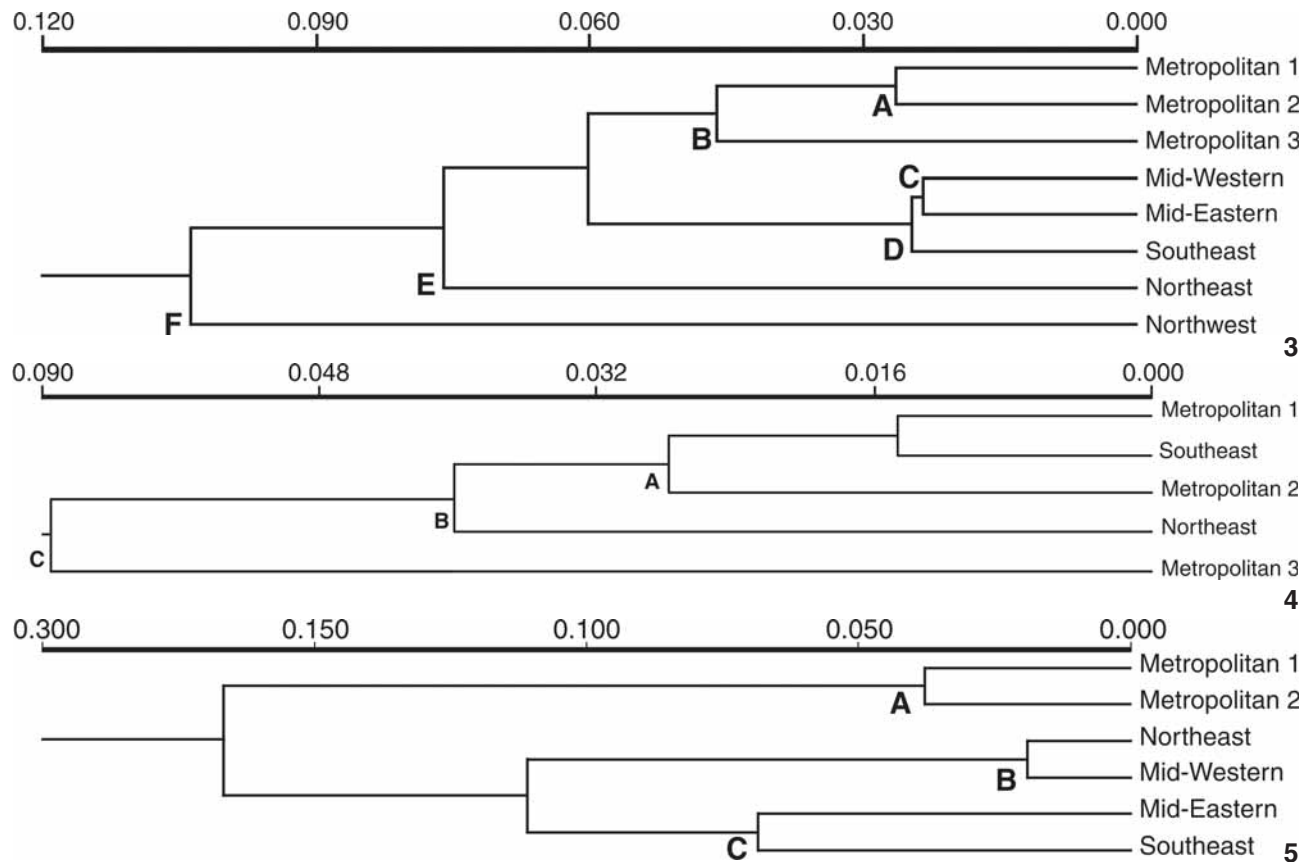
Region	Altitude	Latitude (a)	Longitude	Elytra color pattern						Total	H'	J'	D	
	Mean ± SD	Lower - Higher	Lower - Higher	1	2	3	4	5	6					
Metropolitan														
Porto Alegre	40.3 30.0	29°40'S-30°06'S	50°46'W-51°19'W	0.0534	0.0055	0.6114	0.2376	0.0921	0.0000	543	1.51	0.584	0.442	
Gramado/Canela	72.5 77.1	29°34'S-29°35'S	50°47'W-51°08'W	0.0687	0.0043	0.5236	0.2833	0.1202	0.0000	233	1.67	0.646	0.374	
Osório	16 (b)	29°18'S	49°41'W	0.0496	0.0071	0.7447	0.1064	0.0922	0.0000	141	1.24	0.481	0.577	
Northeast	817 (b)	29°10'S	51°10'W	0.1237	0.0309	0.5567	0.2577	0.0309	0.0000	97	1.66	0.641	0.394	
Southeast	18.0 1.4	31°21'S-31°46'S	51°58'W-52°20'W	0.0603	0.0070	0.5916	0.2135	0.1253	0.0023	431	1.61	0.624	0.415	
			Mean	0.0711	0.0110	0.6056	0.2197	0.0921		1445	1.54	0.595	0.440	
			±SD	0.0303	0.0112	0.0847	0.0683	0.0375			0.18	0.068	0.080	

(a) Latitude and longitude of the sampling places inside of the regions, (b) only one place sampling, (H') Shannon-weaver (J') Index Evenness, (D) dominance index.

Table III. Number, frequency and diversity index of elytra color patterns of *Chauliognathus octomaculatus* in samples sites.

Region	Altitude	Latitude (a)	Longitude	Elytra color pattern		Total	H'	J'	D
	Mean ± SD	Lower - Higher	Lower - Higher	1	2				
Metropolitan									
Porto Alegre	37.5 29.0	29°52'S-29°59'S	50°46'W-51°05'W	0.2419	0.7581	339	0.798	0.798	0.633
Gramado/Canela	57 (b)	29°39'S	50°46'W	0.2041	0.7959	49	0.730	0.730	0.675
Northeast	595.5 440.5	29°26'S-29°29'S	50°35'W-53°59'W	0.4545	0.5455	264	0.994	0.994	0.504
Mid-Western	53 (b)	29°34'S	53°26'W	0.4356	0.5644	101	0.988	0.988	0.508
Mid-Eastern	68 (b)	29°57'S	51°05'W	0.3684	0.6316	133	0.949	0.949	0.535
Southeast	18.0 1.4	31°21'S-31°46'S	51°58'W-52°20'W	0.3000	0.7000	230	0.881	0.881	0.580
			Mean	0.3341	0.6659	1116	0.890	0.890	0.573
			±SD	0.1025	0.1025		0.108	0.108	0.070

(a) Latitude and longitude of the sampling places inside of the regions, (b) only one place sampling, (H') Shannon-weaver (J') Index Evenness, (D) dominance index.



Figures 3-5. Dendrograms constructed using the Manhattan coefficient and the unweighted pair group method with averages (UPGMA) to elytra color patterns from the populations of: (3) *C. flavipes*, (4) *C. fallax*, and (5) *C. Octomaculatus* of Rio Grande do Sul state. Group A-E of figure 3 and Group A-C of figures 4-5, show significant differences between the frequencies of the observed polymorphism ( $p < 0.05$ ).

only in the Northwest region; while the third group is composed of samples from Osório microregion (*Metropolitan 3*).

Similar to the results obtained for *C. flavipes*, the metropolitan region presents groups uniting the Porto Alegre and the Gramado/Canela microregions where the distribution of the coloration pattern frequency is significantly different from that in the microregion of Osório ( $\chi^2$  24.34;  $p < 0.01$ ). As shown in figures 3 and 4 the *C. flavipes* and *C. fallax* populations pertaining to the Osório microregion (*Metropolitan 3*) differ from the other two microregions in relation to the coloration patterns of the elytra.

The lower diversity index in the Osório microregion is the result of the higher frequency (74.47%) of the colour morph 4, and consequently reflects in the domination index of this pattern in relation to the others (Tab. II).

The similarity index calculated based on the frequency of morphs showed, in all populations of *C. fallax*, results similar to those obtained for *C. flavipes* – low dissimilarity ( $< 10\%$ ) amongst all the sampled populations. The greatest difference was between *Metropolitan 3* and the Northeast regions (8.3%)

and the smallest between Metropolitan 1 and the Southeast regions (1.5%), this latter, together with *Metropolitan 2*, making up group A (Fig. 4).

For the *C. octomaculatus* species, samples were taken from nine populations inhabiting five regions to a total of 1116 insects. Only two patterns were found for this species and the pattern 2 was the commonest in all the samples with frequencies between 54% (Northeast) and 79% (Metropolitan 2).

Analysis of the geographic variation of the frequencies of the patterns demonstrated the formation of three clusters for each species (Fig. 5). The first cluster includes the Metropolitan 1 and 2 microregions, the second the Northwest and Mid-Western regions, and the third the Mid-Eastern and Southeast regions. Some of the greatest differences for this species were observed between these regions – for example, the case of the Northeast as compared to *Metropolitan 1 and 2* (21.3% and 25% respectively).

Some location-variable factors (latitude, longitude and altitude) were analyzed to verify what influence they might be having on the diversity levels ( $H'$ ) found in the samples of all

three species. The correlation analysis demonstrated no association between these location variables and the diversities (that is, the overall color variation) of the mentioned *Chauliognathus* species in Rio Grande do Sul. Therefore, although there are differences in the distribution of the coloration patterns in the different regions, these differences do not appear to be influenced by the location-variable factors analyzed here.

However, when we evaluated the Metropolitan region and its three microregions, we found that, as well as the differences in the pattern frequencies, a positive co-relationship existed between an increase in altitude and the occurrence of diversity in *C. flavipes* and *C. fallax* ( $r = 0.860$ ,  $p < 0.01$ ;  $r = 0.974$ ,  $p < 0.01$ , respectively). It should be emphasized that in the other regions differences in altitude did not behave as in the Metropolitan region. In spite of the similar result for both species, the apparent association should be evaluated with caution because we sampled only one population.

## DISCUSSION

The analysis of polymorphism in the *Chauliognathus* species indicates a significant geographic variation in the frequency of the colour patterns all over the area studied. For each species, we observed a general model of variation, and populations near to each other were the most alike, which could be due to similar selective pressures. The differences observed between the samples of the region *metropolitan 3* (microregion Osorio), both in *C. flavipes* and in *C. fallax*, may be due to micro-climatic differences as the sample was obtained near the Northern sea-coast of Rio Grande do Sul.

The presence of spatial variation in polymorphic species indicates that the polymorphism is maintained by the action of natural selection (MAYR 1970, NEVO 1973, OXFORD 1976). Two selective factors may affect the frequency of the forms in a polymorphism: a) Climatic factors and b) factors related to the habitat and the biotics. The variation of climatic factors along the altitude gradient determines gradual changes in the frequency of the forms (BRAKEFIELD 1984, ABBAS *et al.* 1988, THORPE & BROWN 1989). On the other hand, the habitat and biotic factors are more localized and irregular and result in patterns different to those provoked by climatic gradients (MAYR 1970, JONES *et al.* 1977, HALKA & HALKA 1990). The occurrence of frequency variations in polymorphisms along altitude gradients has been registered in many species (BRAKEFIELD 1984, 1985, MCLAIN 1985, THORPE & BROWN 1989). In some polymorphisms, evidence of the action of selective climatic factors on the observed variations was not found (OXFORD 1976, DEARN 1981, BAKER & WOGELZANG 1988).

Notwithstanding of the differences between the regions in the frequencies of the coloration patterns, in the three *Chauliognathus* species, it was not possible to determine what factors might explain the differences, nor how the observed polymorphism was sustained. For such authors as NEVO (1973), JONES *et al.* (1977) and HALKA & HALKA (1990), the action of vari-

ous selective forces, especially in species with extensive distribution areas, would greatly complicate the general descriptions of the observed polymorphisms.

One of the interesting aspects of polymorphism in the species studied is related to the fact that they form a müllerian mimetic ring. In this phenomenon, it would be expected that the pressures exercised by predators would eliminate the rarer types so leading to the appearance and maintenance of a single pattern (monomorphism). In spite of this apparent restriction, a series of examples of polymorphism in müllerian mimics exist (BROWN & BENSON 1974, TURNER *et al.* 1984, BRAKEFIELD 1985, MALLET & JORON 1999, JORON & MALLET 1998, MALLET & JORON 1999, EDMUNDS & GOLDIN 1999).

Therefore, the polymorphism observed in the species studied might be explained, at least in part, by frequency-dependent selection – especially if we consider the density of the aggregates formed by these species (MACHADO & ARAÚJO 1998, 2001). When the size of the population of the prey is large in relation to the number of individuals sacrificed during the learning curve of the predators, selection for the uniformity of the pattern might be relaxed making the occurrence of polymorphism possible (BROWN & BENSON 1974, JORON & MALLET 1998, MALLET & JORON 1999). The fact that the predators apparently need very few tests to associate a particular coloration pattern with an unpalatable prey reinforces this idea. In addition, the similarity between mimic and model (co-mimics) does not need to be very marked – it need only remind the predator of an unpleasant experience (EDMUNDS 1974, TURNER 1977, HUHEEY 1988). Even for Batesian mimics a slight similarity with the model will provide some level of protection (EDMUNDS 1974, LIDNSTROM *et al.* 1997). An additional factor which may favour variation in species with yellow and black coloration, is the innate tendency observed in birds to avoid prospective prey having such colouring (SCHULER & HESSE 1985). An interesting approach was tried by DITTRICH *et al.* (1993), who analyzed the reaction of doves in relation to the diptero (Syrphidae) who imitate wasps but in a very imperfect manner as seen by human eyes. Their results showed that the predators have a considerably capacity for generalization – that is, they do not perceive (or ignore) differences between mimic and model easily distinguishable by the human eye.

Considering the above information and the differences observed between the various coloration patterns found in the *Chauliognathus* species, it appears to be difficult to establish the degree of polymorphism existent. It is possible that some of the differences observed and utilized in the classification of the coloration patterns are not noticed or considered by the predators. If this is happening, some polymorphisms in aposematic species may perhaps in fact only appear to contradict the theoretical principles of müllerian mimicry. This would suggest that the persistence of the coloration patterns may be due to abiotic factors such as temperature, pressure and humidity but in the present state of our knowledge, we cannot be

certain. However, MACHADO & ARAÚJO (1999, 2003) did not find any indication of preferential crossings in *C. flavipes* e *C. fallax* capable of explaining the color polymorphism.

A solution to the polemical discussions on the factors involved in the continuance of polymorphism in müllerian mimics depends in the first place on the elements used by the predators to identify their prey. Basically we must understand the degree of discrimination that the predators have developed – what aspects of the coloration patterns do they take into account when they are learning what they can eat and what not? How important are variations of the degree of palatability in the predator's learning process in real situations? How much variation is actually observed in real populations? Do all of the coloration patterns considered aposematic equally assist the predators to learn what they should eat?

Perhaps the colour polymorphism in the aposematic species is less frequent than it seems to us when seen through the eyes of the predator.

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