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Relationship between labrum sensilla number in the Moroccan locust *Dociostaurus maroccanus* and the nature of its diet

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Abstract

The Moroccan Locust *Dociostaurus maroccanus* is a pest species, regularly harmful to pastures and agricultural output in numerous circum-Mediterranean regions and particularly in Morocco. Species belonging to the same subfamily (Gomphocerinae) are mostly grass-feeding and oligophagous; very few are monophagous or polyphagous. Instars and adults of *D. maroccanus* are characterized by a high degree of polyphagy. Linked to this diet is mandible type; chemoreceptor organs (antenna and palp sensilla) are related to odor or taste (*e.g.*, labrum sensilla). As labrum sensilla plates are correlated with labrum width, we eliminated this source of bias with linear regression statistics. We first studied the genesis of type A sensilla through the different stages of *D. maroccanus*. The relative numbers of A10 increase in adults. Then we tested if the variation of sensilla number relates to the systematic position of the genus or to diet. Comparisons concerned the relative numbers of different sensilla categories in 10 species of acridians. In all its sensilla types, the genus *Dociostaurus* is closer to the mostly polyphagous Oedipodinae than the mostly oligophagous Gomphocerinae. Thus diversification of diet in the genus *Dociostaurus* is linked to an increase in the number of labrum sensilla.

Key words

Dociostaurus, polyphagy, labrum sensilla, chemoreceptor

Introduction

The Moroccan Locust *Dociostaurus maroccanus* (Thunberg) is an acridian species with a tendency to gregarize. It has an economic impact and is the cause of much damage to crops and pastures in many countries of the Mediterranean Basin, including the south of France and the Middle East (Ben Halima 1983, Louveaux & Gillon 1986, Louveaux *et al.* 1996). It is a sedentary species, strictly confined to stony beds, a mosaic vegetation with low cover and a semiarid climate.

In Morocco, *D. maroccanus* occurs in the following three gregarization areas: Askaoun in the Siroua Mountains, Gada Debdou in the northeast of the country and Boulemane in the Middle Atlas Mountains.

The diet of the Moroccan Locust has been investigated, as it has for many acridian species (Williams 1954, Gangwere 1973, Ben Halima 1983, Ben Halima *et al*. 1984, Latchininsky & Launois-Luong 1992, Louveaux *et al*. 1996), with various methods, most frequently feces analysis involving the recognition and counting of plant epidermis remnants.

Most Acrididae are phytophagous but the diversity of the plants consumed arises at the subfamily level, and only rarely at the level of species. Most Gomphocerinae feed on grass and thus are oligophagous (Uvarov 1977, Le Gall 1989). A very few species are monophagous, *e.g.*, *Chorthippus binotatus* Chopard in Western Europe (Bonnet 1997, Picaud *et al*. 1999). However, the Moroccan Locust (instars and adults) and other species of the same genus [*e.g.*, *Dociostaurus genei* (Ocskay)] are characterized by a high degree of polyphagy (involving several plant families). The diversity of the diet is linked to mechanical elements (mouthparts) and to chemoreceptor organs involved in the detection and processing of the food consumed by the insect. The chemoreceptors occur on antennae, palps, hypopharynx and the epipharyngeal face of the labrum (see Haskell & Schoonhoven 1969).

We undertook a quantitative analysis of group A sensilla on the epipharyngeal surface of the clypeolabrum in different species. These dome-shaped sensilla have been demonstrated electrophysiologically to be chemoreceptors in *Schistocerca gregaria* (Forskål) (Haskell & Shoonhoven 1969). Chapman & Thomas (1978) showed that 1) the smallest numbers of A1 sensilla were found in "specialist" species (*e.g.*, *Anablepia* and *Xenocheila* spp. among Gomphocerinae); 2) the same tendency was observed for A3 sensilla numbers but less clearly; 3) in contrast, the numbers of A2 sensilla were similar, irrespective of the feeding habit. The number of labrum sensilla seems thus to be linked to the variety of plants as food resources in Acrididae. The aim of our work was to test if a polyphagous species such as *D. maroccanus* has more labrum sensilla (and which sensilla) than graminivorous Gomphocerinae, and if they are as numerous as in polyphagous Oedipodinae.

Initially, we studied labrum sensilla during the life cycle of the Moroccan Locust (solitary phase, instar 1 to adult stage) in order to understand the genesis of type A sensilla. Then we compared the sensilla complement between the Moroccan Locust and other acridian species, either belonging to the same subfamily (Gomphocerinae) or to the subfamily Oedipodinae. It is well known that most members of these two subfamilies have different diets: most Gomphocerinae are graminivorous (grass feeders) whereas Oedipodinae are graminivorous, forbivorous (dicotyledon feeders) or polyphagous (grass and dicotyledon feeders) (Gangwere & Morales Agacino 1973). We asked if, in regard to its chemoreceptors, *Dociostaurus* is closer to genera belonging to the same subfamily (phylogenetic constraint) or to polyphagous species (functional constraint). As the numbers of type A sensilla vary according to the size of the labrum (Chapman & Thomas 1978), we included

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in our sampling a much smaller species of the genus *Dociostaurus*, *D. genei* (Ocskay) having a polyphagous diet as in *D. maroccanus*.

Material and methods

The collection locales of the 10 studied species are as follows: *Oedipoda coerulescens* (Linnaeus): Bessines-sur-Gartempe, Haute-Vienne, France, October 1995; *Acrotylus insubricus* (Scopoli): Gordes, Vaucluse, France, August 2000; *Stethophyma grossum* (Linnaeus): Marval, Haute-Vienne, July 1991; *D. genei*: Gordes, Vaucluse, August 2000; *D. maroccanus*: Al-Azaghar, Middle Atlas Mts, Morocco, June 2000; *Chrysochraon dispar* (Germar): Davignac, Corrèze, France, August 1999; *Euchorthippus declivus* (Brisout-Barnville): Champeaux, Dordogne, France, July 1998; *Chorthippus dorsatus* (Zetterstedt): Bessines-sur-Gartempe, Haute-Vienne, October 1995; *Chorthippus parallelus* (Zetterstedt): Couzeix, Haute-Vienne, September 1995; *Chorthippus biguttulus* (Linnaeus): Bessines-sur-Gartempe, Haute-Vienne, October 1995. For each sex and species, five individuals were studied.

In the case of *D. maroccanus* (solitary phase), we investigated five individuals of each sex and stage from 3rd instar to adult and ten individuals (of undetermined sex) of each of the two first instars. It would be interesting to investigate the type A sensilla of the gregarious phase of *D. maroccanus*, in relation to its diet; unfortunately, we did not have the opportunity to study gregarious phase individuals.

The classification (Oedipodinae or Gomphocerinae) and diet of the acridian species, as determined from the literature, are given in Table 1. We added data from personal unpublished observations, taking into account the feces produced by 12 individuals collected in the field, as follows: *D. genei*, August 2000, near Gordes on dry and low vegetation (Vaucluse, France) [feces of the different individuals were pooled and stored in alcohol]; *S. grossum*, collected in humid prairies September 1997 at Barsanges (Corrèze, France) and September 1994 at Sauvagnac (Haute-Vienne, France) [feces of the different individuals were analyzed separately].

Each labrum was dissected under a stereomicroscope and immersed into 50% KOH solution for 1-6 h in order to clear the soft tissues, then rinsed in distilled water for 15 min. The labrum was mounted in glycerol gelatin under a cover glass, observed under a microscope, and labrum size measured.

Thomas (1966) has defined four discrete groups of sensilla, characterized by their position on the epipharyngeal surface (Fig. 1): type A1 (proximal end), A2 (central part), A3 (distal end) and A10 (lateral part, at a level intermediate between A1 and A2 groups). These sensilla groups can easily be recognized in the different species. In the case of the A3 group, the sensilla can be lacking in some species, and are either replaced by vestigial structures such as spines or a flat surface.

Labrum width was measured and the different sensilla types (A1, A2, A3 and A10) counted. The counts of sensilla numbers represent totals of the groups on both sides of the labrum.

Statistical analyses (ANOVA, regression analysis) were performed with SYSTAT 7.0 (SPSS Inc. 1997). We verified the normal distribution of all the variables before applying parametric tests. In the case

Table 1. Diet of the studied species.

Subfamily	Species	Dicots	Poaceae	Cyperaceae	Juncaceae	Ref.
Oedipodinae	*Oedipoda coerulescens*	■	▒			4
	Acrotylus insubricus	▒	■	▒	▒	4,6
	Stethophyma grossum		■			2
Gomphocerinae	*Dociostaurus genei*		■			2,4
	D. maroccanus	■	■			5
	Chrysochraon dispar		■			3
	Euchorthippus declivus		■			1
	Chorthippus parallelus		■			1,2,3
	Chorthippus dorsatus		■			2
	Chorthippus biguttulus		■			1,2,3

■ Dominant food source ▒ Minor food source

1. Bonnet 1997; 2. Petit, unpublished; 3. Guéguen 1976; 4. Gangwere and Morales Agacino 1973; 5. Ben Halima *et al.* 1984; 6. Launois-Luong 1979.

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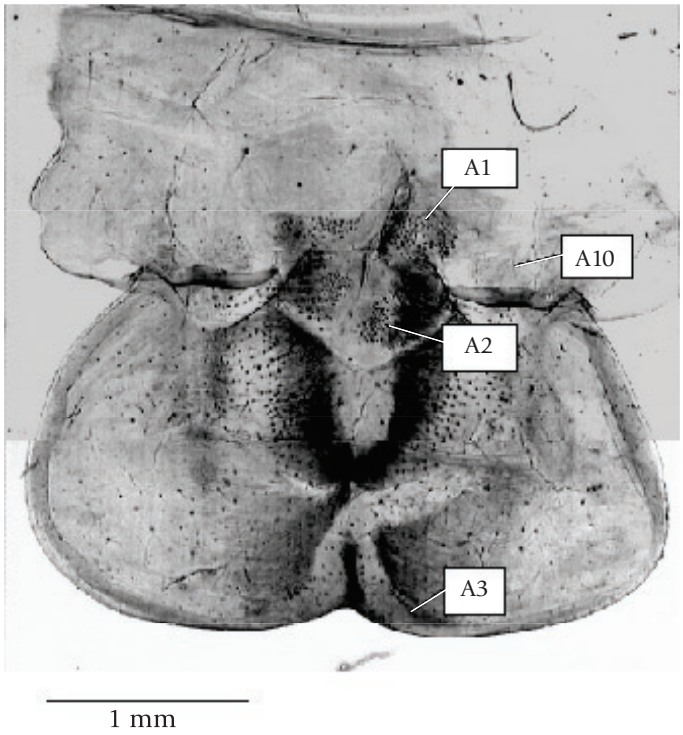


Fig. 1. Position of type A sensilla on the epipharyngeal surface of the labrum in male *D. maroccanus.*

of the variables "A10" and "A10 residues", we log-transformed the values to normalize their distribution. We used regression analysis to calculate the residuals which give a measure of deviation of each point from the regression line.

Results

Diet of the studied species.— The diet of *S. grossum* was as follows: Barsange site: *Poa pratensis* (8.3%), *Agrostis canina* (12.3%), *Holcus lanatus* (30.0%), undetermined Poaceae (24%), *Carex* spp. (3.7%) and *Juncus effusus* (21.3%). In summary, Poaceae represent 75% of total consumed plants, Cyperaceae 3.7% and Juncaceae 21.3%. The ground-cover dicotyledons (7 species) were about 20% of the total. Sauvagnac site: *Holcus lanatus* (58.8%), *Agrostis canina* (25.2 %), *Dactylis glomerata* (1.8%), *Festuca rubra* (13.8%), *Molinia caerulea* (1.3%), *Carex* spp. (13.9%) and *Juncus effusus* (24.5%). In summary, Poaceae represent about 72% of total consumed plants, Cyperaceae 10% and Juncaceae 14%. Ground cover by Poaceae was 41%, for Cyperaceae 9%, Juncaceae ∼ 14% and dicotyledons (11 species) 36%.

Taken together, these results show that *S. grossum* is a monocotyledon feeder. This insect species makes a food choice, as dicotyledons are totally absent in its diet, although significantly present in the environment.

The diet of *D. genei* was not as thoroughly determined as in the previous case: three different species of Poaceae represented 18.75% of total consumed plants, eight species of dicotyledons the remaining part (81.25%). As the ground cover of each plant species was not recorded, we cannot assume that the distribution of plant remains in the feces reflects the abundance of plants in the field. Nevertheless, *D. genei* is a polyphagous species.

Variations of labrum sensilla number during developmental stages.— In *D. maroccanus* the number of type A sensilla varies as a function of developmental stage (Fig. 2). The numbers of type A1, A2 and A3 sensilla increase, especially during instar three. Type A10 sensilla are lacking in the first two instars, their number remaining quite constant during instars 3-5, with a sudden increase in adults. It should be noted that the overall increase in type A3 sensilla number is very slight in comparison to that of the other sensilla (from 47 in instar one to 75 in the adult).

For *D. maroccanus*, numbers of type A1, A2, A3 and A10 sensilla are highly correlated with labrum width (n = 60, Pearson r = 0.96, 0.89, 0.72 and 0.79 rcɔpectively, $p < 0.001$). And the same is true of the other (10) acridian species: labrum width correlates with the number of type A1, A2, A3 and A10 sensilla (n = 95, Pearson r = 0.78, 0.70, 0.61 and 0.76 respectively, $p < 0.001$). In the literature, *e.g.*, Chapman 1982, labrum surface area is usually estimated by labrum width squared. We verified here that this estimate does not give a better correlation with sensilla numbers than simple labrum width (Table 2).

Because labrum width increases during development, it is useful to calculate the regression residuals between numbers of type A sensilla and labrum width in order to eliminate size effect (Figs 3a, b). We performed four multiway ANOVA with stage and sex as factors. These tests revealed that the effect of sex is not significant (n = 60, $p > 0.24$). The effect of stage is significant for relative numbers of A10 (log-transformed) (n = 60, p = 0.005) and type A3 sensilla (n = 60, $p < 0.001$). These differences are mainly due to the relatively high numbers of A3 in instar 2 and of A10 in the adult. In contrast, the differences are not significant for A1 and A2 (n = 60, p = 0.62 and p = 0.40 respectively).

Variations of labrum sensilla number in different species.— The numbers of sensilla in adults show a great interspecific variability (Fig. 4). At first sight, the largest species have the most numerous sensilla. We verified (data not shown) that this observation is true within each species where there is a sex dimorphism concerning body size. The numbers of sensilla, from the most to the least numerous, occur in A1, A2, A3 and A10 groups. In graminivorous Gomphocerinae A10 sensilla are often lacking.

As above, these studies retain labrum width as a predictor of sensilla numbers. The relationships are highly significant (n = 95, Pearson $r > 0.60$, $p < 0.001$, in the four cases) and illustrated in Fig. 5. Linear regression equations (Fig. 5) were used to calculate the residuals in order to remove the size effect.

Regarding sensilla relative numbers (Fig. 6), A2 and A3 relative numbers show parallel variation, suggesting linked functions. In contrast, A1 and A10 relative numbers show variations independent from each other and from the other sensilla.

The Oedipodinae show very contrasting organizations of relative numbers of labrum sensilla. *Oedipoda* has generally positive (above regression lines) numbers for any category of sensillum. *Acrotylus* residuals are close to the regression line, except for A10 numbers, which are clearly above. *Stethophyma* has a positive number of A1 sensilla, but negative numbers (under the regression line) of A2 and A3 types. The situation in Gomphocerinae is more homogeneous and two groups are distinct: *Dociostaurus* (*D. maroccanus* and *D. genei*) having generally positive numbers of sensilla, and the remaining species of *Chrysochraon*, *Euchorthippus* and *Chorthippus* having generally negative numbers of sensilla.

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In summary, it should be noted that both species of *Dociostaurus* have relatively greater numbers of sensilla than the remaining Gomphocerinae and thus are closer to *Oedipoda* in the Oedipodinae.

Discussion

Variations of sensilla during D. maroccanus development.— Our regression analyses agree with the results found in *Catantops*, *Chortoicetes*, *Locusta* and *Melanoplus* as reported in Chapman & Thomas (1978), *i.e.*, correlation coefficients are higher between labrum size and the numbers of A1 and A2 sensilla than of A3. However, all correlations were highly significant (Table 2). If the number of sensilla increases regularly during development, the withdrawal of size effect shows that adults possess relatively more A10 sensilla than do instars. The variations of A3 sensilla numbers are not clear.

D. maroccanus has a wide range of food sources. Ben Halima (1983) and Ben Halima *et al.* (1984) showed that during development at the station of Gada Debdou (Morocco), the first three stages eat a small number (14) of plant families, with grass as the major portion. During the 4th instar, more so in the 5th instar and adult, the food portion from dicotyledons increases. Ultimately, adults feed on 39 plant species. Such diversification of the diet during the life of acridians has been described in other species (Bernays & Chapman 1970).

We can hypothesize a link between the variations of sensilla numbers and diet. The significance of absolute values of A1 and A2 sensilla numbers (n = 100, Pearson r = > 0.60 and p < 0.001) seems to be greater than relative values. The burst increase of the relative numbers of A10 sensilla in the adult could be linked to the diversification of diet.

Interspecific variation in sensilla.— Absolute values of sensilla numbers are irrespective of diet and depend on the size of the species: the range of values of *D. genei* is closer to other Gomphocerinae than to *D. maroccanus*. Correlation analyses show that A1 and A10 sensilla vary tightly with labrum width, more than A2 and A3 sensilla do. These observations agree with the literature (Chapman & Thomas 1978) except for A2 sensilla.

Table 2. Pearson correlation coefficients between numbers of sensilla, width of labrum and squared labrum width.

	D. maroccanus		10 species	
	n = 60, p < 0.001		n = 100, p < 0.001	
	Width	Width^2	Width	Width^2
A1	0.96	0.93	0.78	0.78
A2	0.89	0.87	0.7	0.74
A3	0.72	0.72	0.61	0.65
A10	0.79	0.83	0.76	0.75

Relative values of sensilla numbers will be taken into account in the following. The studied graminivorous species (*C. dispar, C. dorsatus, C. parallelus, C. biguttulus* and *E. declivus* in Gomphocerinae) possess the smallest relative number of A1 sensilla. *Acrotylus* residuals are close. Thus the relative number of A1 sensilla in *D. genei* is close to the number present in *O. coerulescens* and *S. grossum* (Oedipodinae).

The situations with A2 and A3 sensilla are quite comparable. The monocotyledon feeders have, in general, relatively low numbers of sensilla, except for relative numbers of A3 in *Chorthippus* spp. *S. grossum* belongs to the same group as grass-feeding Gomphocerinae. Both species of *Dociostaurus*, and especially *D. maroccanus*, have relatively high numbers of sensilla, as in *O. coerulescens*. As for A10 relative numbers, *D. genei* shows a high value, as in the polyphagous Oedipodinae.

Finally, the studied species of *Dociostaurus* have generally higher relative numbers of sensilla than graminivorous Gomphocerinae. However, the A10 relative numbers seem to be most correlated with polyphagy (*O. coerulescens*, *A. insubricus* and *Dociostaurus*). This observation should be tested with additional polyphagous Oedipodinae.

We hypothesize that polyphagy in the genus *Dociostaurus* requires a great number of type A sensilla. The importance of sensilla on the epipharyngeal surface of the labrum of acridians seems to be a determinant element in the recognition of nutrient composition.

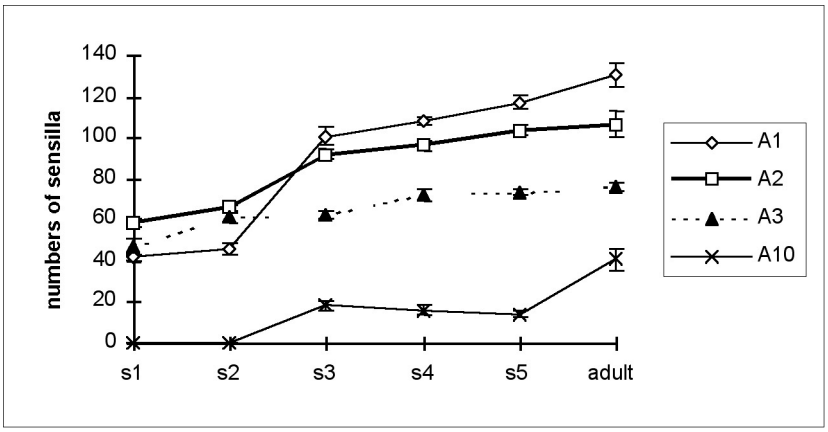


Fig. 2. Means ($\pm s_{\bar{x}}$) of type A sensilla in the different instars of *D. maroccanus;* s1, s2, *etc.* designate successive stadia.

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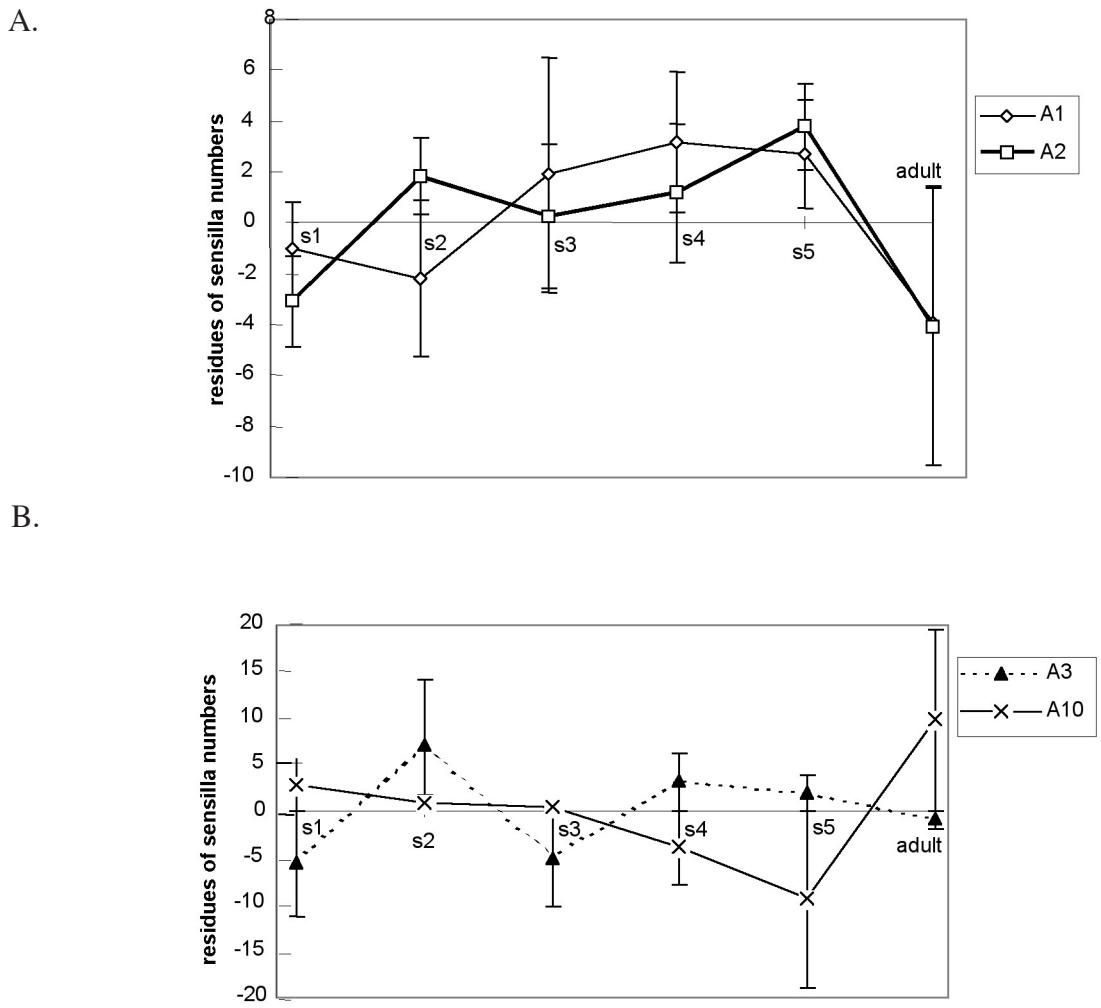


Fig. 3. Mean ($\pm s_{\bar{x}}$) of sensilla numbers in the different stadia (s1, s2 *etc.*) of *D. maroccanus.* 3a. A1 and A2 sensilla; 3b. A3 and A10 sensilla.

Sensilla and diet.— It is generally held that specialization of diet is linked to a decrease in the number of labrum sensilla, especially for A1, A2 and A3 groups (Chapman & Thomas 1978, Chapman 1982). The example of *Dociostaurus,* studied here for the first time, demonstrates that the converse is also true, *i.e.*, the number of sensilla can increase when the diet becomes more diversified: the insect has to face a great number of stimuli coming from the diverse plant leaf surfaces and tissues.

As most Gomphocerinae are graminivorous, it is probable that the polyphagous genus *Dociostaurus* has evolved from graminivorous species. The fact that the first instars of *D. maroccanus* eat grass preferentially supports this view. The evolutionary plasticity of sensilla number has allowed an increase in sensilla in relation to the diversification of sources of food. As Haskell & Shoonhoven (1969) demonstrated in *Schistocerca* and *Locusta*, A1 and A2 sensilla could be linked to the perception of phagostimulant molecules, such as sugars, whereas A3 sensilla could be linked to deterrent molecules. The importance of the number of A3 in the response is not clear. It should be tested whether the function of the sensilla in *Dociostaurus* is consistent with their function in both *Schistocerca* and *Locusta.*

Latchininsky & Launois-Luong (1992) report that the gregarious phase of *D. maroccanus* has a more diversified source of food than the solitary phase. For example, gregarious individuals can even feed on *Pinus* and *Juniperus*. We hypothesize that these insects will present a modification of their A sensilla composition, and especially an increase in relative number of the type A10. However, the link between diet and the numbers of labrum sensilla can be otherwise, as demonstrated in the example of *Chorthippus binotatus* (Picaud *et al*. 1999), a specialist gomphocerine feeding on Fabaceae bushes.

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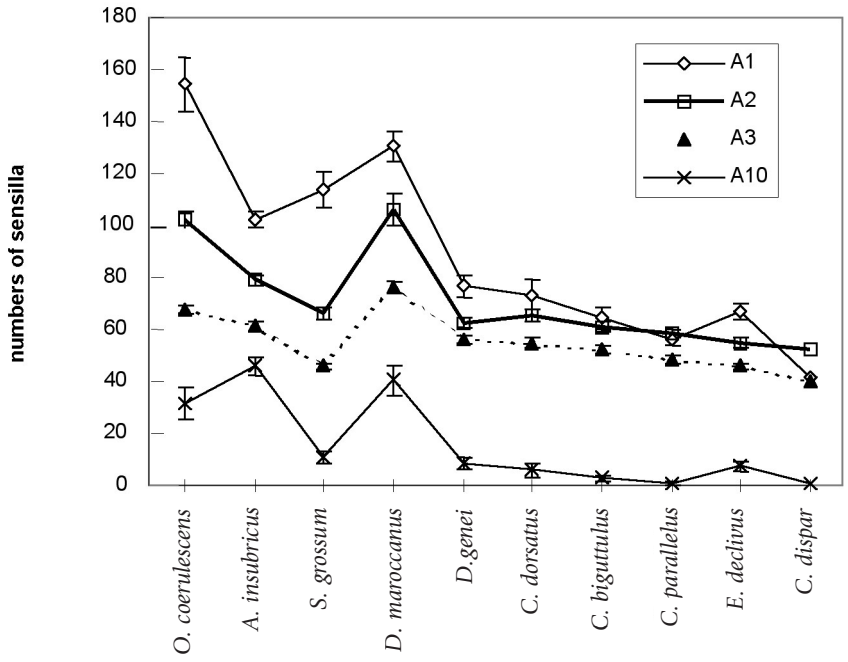


Fig. 4. Means ($\pm s_{\bar{x}}$) of group A sensilla in 10 species of adult Acrididae. The three leftmost are Oedipodinae, the remaining Gomphocerinae. The order of species does not reflect a ranking by size but by systematic relationship. The connecting lines between the points help visualize variations within each sensilla type.

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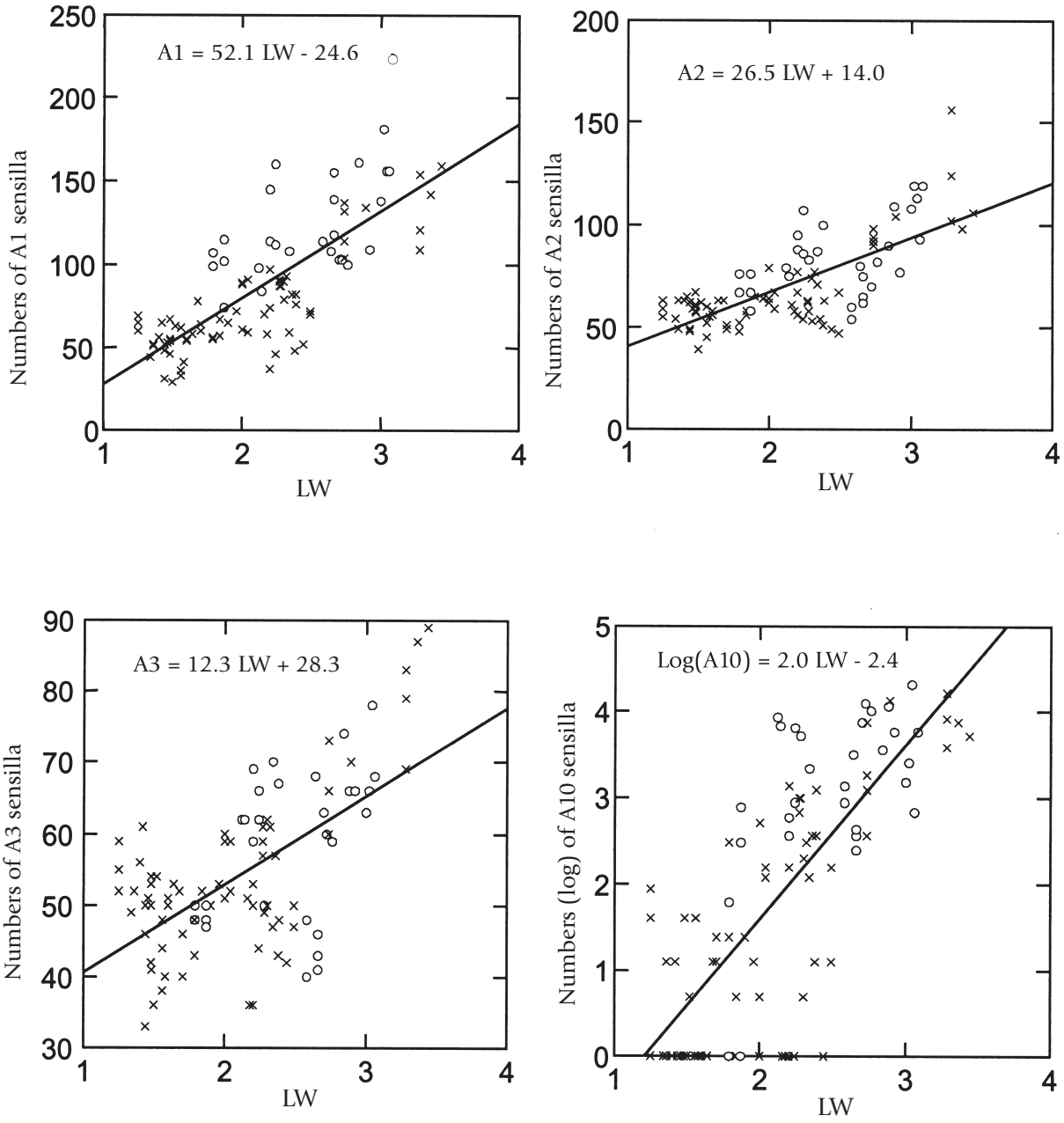


Fig. 5. Relation between labrum width (LW) and numbers of sensilla for 10 studied species. In all cases, n = 100 and $p < 0.001$. o = Oedipodinae; x = Gomphocerinae

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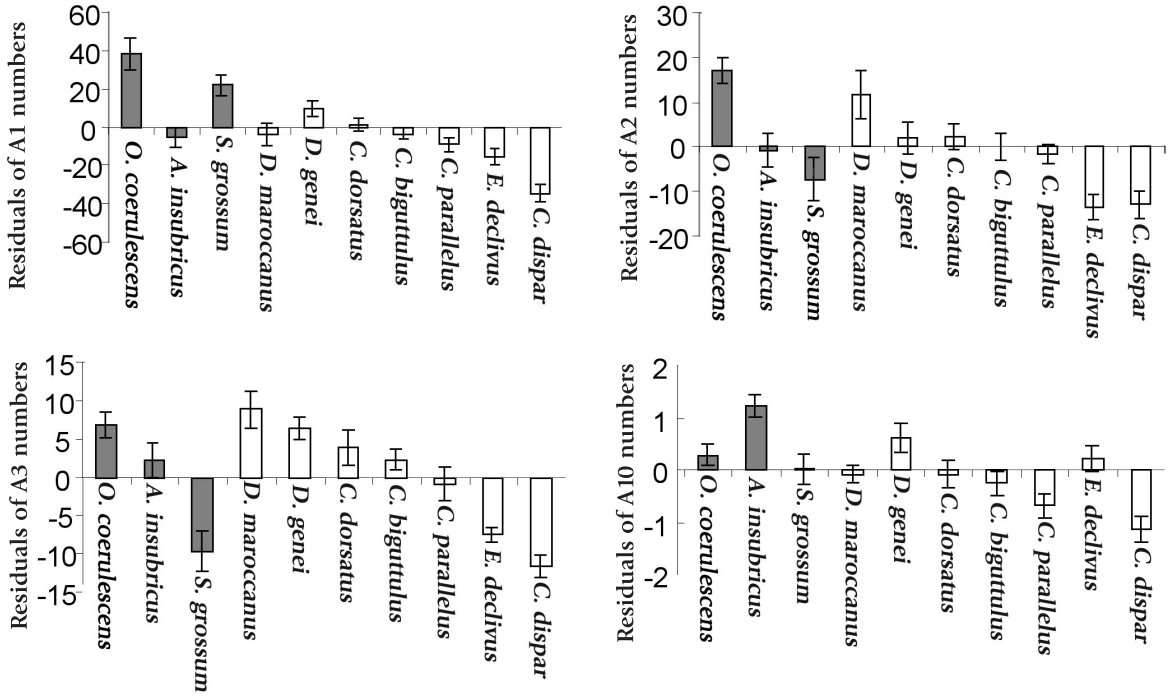


Fig. 6. Mean ($\pm s_{\bar{x}}$) of sensilla numbers in 10 species of Acrididae. Positive and negative numbers correspond to absolute values above and under the regression line respectively (see Fig. 5). Grey bars: Oedipodinae; open bars: Gomphocerinae.

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