

**THE RELATIONSHIP BETWEEN ECOLOGICAL CAPACITY AND
MORPHOMETRY IN A NEOTROPICAL COMMUNITY OF
PASSALIDAE (COLEOPTERA)**

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Abstract

The relationship between diverse morphometric and ecological variables are studied in a neotropical community of Passalidae. Species which exploit log underbark exhibit a body of less relative thickness and less relative width than those that inhabit sapwood/heartwood. It is possible that the former species are more generalist in their use of resources because they present larger populations and exploit a greater number of tree species; furthermore, their seasonal niche is wider and the strategies they employ are different. The authors consider that the occupation of two structurally and materially different parts of the same host could mark the most important ecological segregation for these insects, which likely appear quickly in the evolutionary history of Passalidae.

Choice of microhabitat between log underbark and sapwood/heartwood seems to depend largely on the morphometry of Passalidae. This relationship, mentioned briefly by specialists of the neotropical region (Schuster 1978, Reyes-Castillo and Halffter 1984), has been studied in 20 species of Oriental and Australian passalid beetles (Johki and Kon 1987). Is simple and foreseeable: the thickness/width ratio (flattened vs. convex form) is less for species inhabiting log underbark. This is clearly a morphological adaptation selected for the requirements of a particular environment.

Although there are no related studies to date, it has been postulated that underbark inhabitants are capable of wider dispersion than sapwood/heartwood dwellers due to their aerodynamic superiority as well as to the ephemeral nature of the underbark habitat (Reyes-Castillo and Halffter 1984, Boucher 1991). In this case, body shape would influence the species' other ecological capacities. This possibility has not yet been tested due to the dearth of data regarding ecological passalid communities.

Using data gleaned from an exhaustive study (Castillo 1987) of the passalid community in a tropical evergreen forest in Los Tuxtlas (Veracruz, Mexico), this study aims to i) examine the general morphometry of species in a neotropical community; ii) determine if certain ecological characteristics of these species are related to their shape.

Methods

Description of the Zone. The study was carried out in the area surrounding the Estación de Biología Tropical in Los Tuxtlas, belonging to the Universidad Nacional Autónoma de México, in the southeastern region of the state of Veracruz between 95°04' and 95°09'W and 18°34' and 18°36'N. The altitude ranges from 150 to 530 m above sea level. The climate is warm and humid with a mean annual temperature of 24°C (ranging from 20° to 28°C) and mean annual rainfall of 4,900 mm, the dry season running from March to May and the humid season from June to February. The pristine vegetation characteristic of the zone is tropical evergreen forest.

Sampling Method. The data used originate from 15 sampling periods carried out every 30–45 days between May of 1984 and October of 1986. Each sampling required an average of four days' field work, during which the fauna contained in fallen trunks was meticulously captured by hand. The number of logs examined during each sampling period varied, oscillating between 4 and 30 with an average of 15.60 ± 2.04 SE logs. A total of 234 fallen trunks belonging to 45 plant species were examined; in total, 2,971 passalid individuals from 12 different species were obtained. On the basis of these general data (Castillo 1987), a series of variables has been calculated for each of the species (Table 1): i) the average number of individuals per trunk ($\bar{N} \pm SE$), ii) their relative presence in different species of known trees, trophic frequency (TF), iii) the Levins' measure of standardized niche breadth (Krebs 1989) according to the 15 sampling periods or seasonal niche breadth (SNB), and iv) their relative presence in the interior of trees (sapwood-heartwood), microhabitat frequency (MF). With respect to body measurements, the following were taken: body length (L), elytral width (W), metathoracic body height or body thickness (H), and fresh body weight (BW). The first three measurements were estimated for 10 individuals from each species, while body weight was estimated based on variable numbers of individuals (between 7 and 36).

Results and Discussion

Morphometry and Body Weight. There are significant positive correlations between L, W and H with $P < 0.001$ in all cases ($df = 11$): L and W ($r = 0.996$), L and H ($r = 0.931$), W and H ($r = 0.948$). It is obvious that a linear increase in any of these measurements is linked to an increase in the others. A positive correlation also exists between length and body weight as well as a significant linear regression (Fig. 1). The power regression between these variables is used frequently in insects to estimate the weight of an insect on the basis of its size (Jarošík, 1989, Rogers *et al.* 1976 and 1977). In this case, the linear regression provides more accurate biomass predictions (t-statistic for $b = 14.988$; $S_{yx} = 0.137$) than power ($t = 9.974$; $S_{yx} = 0.267$) or exponential ($t = 8.345$; $S_{yx} = 0.313$) regressions. This fact is not anomalous and occurs when the species in question have a similar morphometric groundplan (Lobo 1993), as seems to be the case for Passalidae.

The W/L ratio remains practically constant (between 0.307 and 0.330) regardless of body length and the subfamily to which the species belongs (Fig. 2). However, the H/W ratio differs considerably, being higher for Proculini ($\bar{x} \pm SE = 0.714 \pm 0.015$) than for Passalini (0.607 ± 0.025) ($t = 3.63$, $df = 10$, $P = 0.005$). Thus, the body shape of the passalid beetle seems to be relatively uniform throughout all regions of the world, as the W/L ratio for Oriental and Australian species oscillates between 0.3 and 0.4 (Johki and Kon

Table 1. Average number of individuals per trunk ($\bar{N} \pm SE$), relative presence in distinct species of known trees (TF), seasonal niche breadth (SNB), microhabitat frequency (MF), body length (L), elytral width (W), body thickness (H), and fresh body weight (BW) for the 12 species of Passalidae.

	\bar{N}	TF	SNB	MF	L	W	H	BW
Passalini								
<i>Paxillus leachi</i>	1.73 ± 1.29	0.244	0.285	0.12	18.9 ± 0.2	5.8 ± 0.1	3.1 ± 0.1	0.21 ± 0.01
<i>Passalus caelatus</i>	1.28 ± 0.54	0.400	0.585	0.68	15.1 ± 0.2	4.9 ± 0.1	3.0 ± 0.1	0.13 ± 0.00
<i>P. inops</i>	0.04 ± 0.04	0.089	0.104	1	29.8 ± 0.4	9.2 ± 0.1	6.2 ± 0.1	1.27 ± 0.29
<i>P. punctatosiratus</i>	4.30 ± 1.21	0.689	0.760	0.60	23.1 ± 0.3	7.5 ± 0.1	4.9 ± 0.1	0.47 ± 0.02
<i>P. interstitialis</i>	0.56 ± 0.91	0.133	0.030	0	27.8 ± 0.4	8.5 ± 0.1	4.6 ± 0.1	0.70 ± 0.03
<i>P. punctiger</i>	3.58 ± 4.17	0.267	0.109	0.35	38.3 ± 0.4	12.0 ± 0.1	7.5 ± 0.1	1.93 ± 0.05
Proculini								
<i>Spurillus bicornis</i>	0.01 ± 0.02	0.089	0.064	1	18.1 ± 0.2	5.8 ± 0.1	3.9 ± 0.04	0.49 ± 0.01
<i>Popillius mysticus</i>	0.16 ± 0.29	0.022	0.014	1	25.4 ± 0.4	8.0 ± 0.1	5.8 ± 0.1	0.72 ± 0.02
<i>O. striatopunctatus</i>	0.63 ± 1.06	0.067	0.025	1	27.1 ± 0.3	8.8 ± 0.1	6.3 ± 0.1	0.84 ± 0.03
<i>Heliscus tropicus</i>	0.12 ± 0.23	0.044	0.001	1	27.4 ± 0.5	9.0 ± 0.1	6.5 ± 0.1	0.84 ± 0.03
<i>Verres corticicola</i>	2.33 ± 0.93	0.533	0.606	0.92	32.8 ± 0.4	10.3 ± 0.1	7.9 ± 0.2	1.47 ± 0.03
<i>V. cavicollis</i>	0.54 ± 0.65	0.089	0.098	1	38.8 ± 0.4	12.6 ± 0.1	8.5 ± 0.1	1.94 ± 0.06

Table 2. Spearman rank correlation coefficient values between the morphometric and ecological variables considered. *0.01 < P < 0.05. **0.001 < P < 0.01.

	L	W	H	BW	W/L	H/W	N	TF	SNB
N	0.06	0.04	0.05	-0.08	-0.15	-0.29			
TF	-0.06	-0.12	-0.17	-0.23	-0.31	-0.45	0.782**		
SNB	-0.08	-0.11	-0.15	-0.19	-0.27	-0.35	0.706*	0.937**	
MF	0.08	0.21	0.37	0.37	0.62*	0.75**	-0.694*	-0.703*	-0.515

*0.01 < P < 0.05.
**0.001 < P < 0.01.

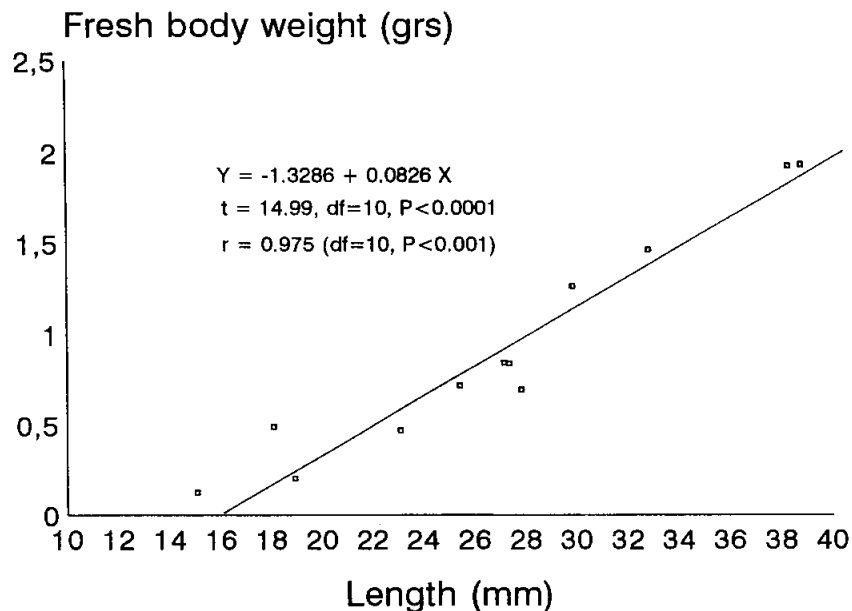


Fig. 1. Length-weight ratio and linear function for the 12 species of Passalidae.

1987). That is, width tends to equal one third of length. This homogeneity in passalid morphometry is probably because these beetles are highly adapted to their microhabitat: when the general size is large, as it is in the Proculini (between 1 and 6 cm), the occupation of tree interiors may require long body shape. In spite of this uniformity, there is much variation between body thickness among species (flattened vs. convex form); there is also a significantly different H/W ratio between higher taxonomic groups. In the New World, the two tribes Passalini and Proculini differ in body thickness, as do the three subfamilies present in the Oriental and Australian regions, Aulacocyclusinae, Macroliniinae and Leptaulacinae (Johki and Kon 1987). It is implicit that higher taxa are older than lower taxa.

Thus, the fact that this contemporary pattern is expressed at a high taxonomic level suggests that it was established a long time ago. Geographically distant taxa with similar morphometry can be interpreted as the result of the adaptation to similar resources and ecological conditions, or as the result of shared ancestry. In the case of the passalids the morphometric convergence occurs between higher and likely phylogenetically distant taxa. For these reasons: i) this morphometric pattern likely appeared quickly in the evolutionary history of Passalidae, ii) it is likely that it arose independently on two or several occasions, and iii) it is likely that it is the result of an ecological adaptation. The use of equal trophic resources could lead to the same morphometric result in phylogenetically and geographically distant lines. Morphometry and ecology are highly associated in this group.

Morphometry and Ecological Capacities. No statistically significant correlations exist between any morphometric variables and the average number of individuals per tree (\bar{N}), frequency in different species of trees (TF), or

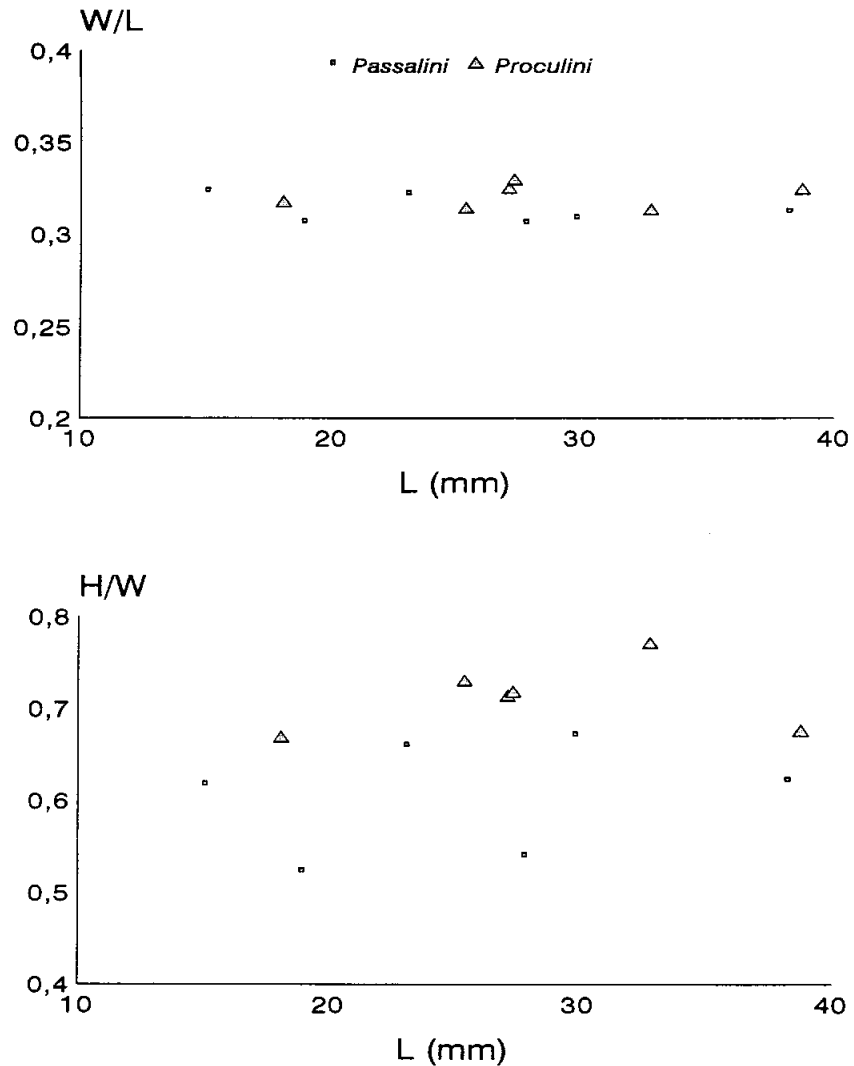


Fig. 2. Distribution of the W/L and H/W ratios according to body length for the 12 species of Passalidae.

seasonal niche breadth (SNB). In contrast, microhabitat frequency (MF) is positively correlated, both with the W/L and H/W ratios (Table 2). It is highly probable (Spearman rank correlation coefficient, $r_s = 0.75$; $P = 0.013$) that thicker species appear more frequently in the internal part of the trunk. Sapwood/heartwood inhabitants would also exhibit rounder body shapes ($r_s = 0.62$; $P = 0.041$). The conclusion drawn from this analysis is that the generalist vs. specialist character of the species (measured by \bar{N} , TF and SNB) relates neither to any linear measurement nor to morphometry. Furthermore, micro-

habitat preference does not correspond to any linear measurement; rather, it is related to morphometry. The species which exploit log underbark have less relative thickness and smaller relative width than sapwood/heartwood inhabiting species.

Strong positive correlations exist between abundance (\bar{N}), tree frequency (TF) and seasonal niche breadth (SNB) (Table 2). The three variables may, in fact, be intimately related. There are no existing species with abundant populations, being restricted to few types of trees or to certain months. In other words, seasonal or trophic specialization (dependent on tree type) does not seem important for Passalidae, at least not for those that live in dicotyledonous angiosperms (Reyes-Castillo 1970, Schuster 1978). Statistically important negative correlations do exist between some of these variables and microhabitat frequency (MF). Although weak, these correlations suggest the possibility that species which exploit the outer parts of the tree (lower MF) exhibit the greatest degree of generalization (greater \bar{N} , TF and SNB).

The external parts of fallen logs are much more putrescent, being subject to more activity by climatic agents (Graham 1925, Savely 1939); they are also more vulnerable to the access of passalid predators and parasites. These microenvironmental characteristics of bark have favored adaptive strategies which increase dispersion capacity and population size and also influence the life style of underbark-inhabiting species, a life style which differs greatly from that of sapwood/heartwood inhabitants. The family group of passalids living in the log interior is more integrated. This unity (a bisexual pair and offspring) is the direct result of the habitat itself. In underbark-inhabiting passalids, on the other hand, some family groups do not remain totally isolated from other groups. Here again, microhabitat exercises its influence and families interact, even forming an occasional common nest. Underbark passalids seem to respond to the ephemeral nature of resources, as the grouping of organisms (for example, the laying of many eggs, Morón *et al.* 1988) represents a mechanism of defense against the most common predators and parasites present in this type of habitat.

This could provide the biological explanation for why underbark species are more generalized in their use of resources. The exploitation of inner tree trunks by sapwood/heartwood inhabitants, in contrast, favors ecological specialization. In the New World, the only known types of Proculini which exploit underbark are the "thicker" species. These have diversified in the Mexican Transition Zone; they are characteristic of higher altitudes than neotropical Passalini, and frequently exhibit wing reduction, which favors the production of sounds linked to their subsocial behavior (Reyes-Castillo 1970, Reyes-Castillo and Halfpeter 1978).

The specialized life style of Passalidae which inhabit fallen trunks may account for their long, round shape; while the type of material consumed in the fallen log (underbark vs. sapwood/heartwood) is linked to variation in body type, being either flattened or convex. The exploitation of two different parts of the same material seems to mark the most important ecological segregation for these insects, capable even of conditioning essential ecological characteristics in the species (generalization/specialization). We consider that the importance of this ecological segregation is corroborated by the early and universal evolution in the phylogenetic history of this group: "early" because the variation in passalid body thickness corresponds to taxonomically higher groups (tribes, subfamilies or families); "universal" because the ecological segregation appeared independently in biogeographically distant locations.

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