Feeding habits and range of body size : a case study in Papua New Guinea using arboreal leaf-beetles and weevils (Coleoptera : Chrysomelidae, Curculionidae)

PDF erstellt am: **20.09.2024**

Feeding habits and range of body size: a case study in Papua New Guinea using arboreal leaf-beetles and weevils (Coleoptera: Chrysomelidae, Curculionidae)

YVES BASSET[1,2], NEIL D. SPRINGATE[3] & G. A. SAMUELSON[1]

[1] Department of Natural Sciences, Bishop Museum, PO Box 19000A, Honolulu HI 96817-0916, USA
[2] Present address: Christensen Research Institute, PO Box 305, Madang, Papua New Guinea
[3] Département d'Entomologie, Muséum d'Histoire naturelle, CP 6434, CH-1211 Genève 6, Switzerland

We measured the intraspecific range of body size (defined by the ratio maximum : minimum lengths in a population with at least 10 individuals) of 33 and 39 adult morphospecies of Chrysomelidae and Curculionidae, respectively, obtained from a localized area in Wau, Papua New Guinea. Exclusively, beetles were collected from the foliage of 10 tree species using various sampling methods. Live adults were used in feeding experiments to assign each morphospecies to one of the four following categories: (1) specialist leaf-feeder; (2) generalist leaf-feeder; (3) leaf-feeder, unknown; and (4) wood-borer. Our analyses suggest that feeding category exerted the greatest influence on the range of body size, whereas the effects of body size per se, number of individuals available for analysis and taxonomic category were less evident or absent. In general, leaf-feeders showed a lower range of body size than wood-borers, and leaf-feeding specialists showed a lower range of body size than generalists. In particular, slopes for the regression of minimum against maximum lengths measured, calculated by the method of the reduced major axis, were significantly higher for wood-borers than for leaf-feeding specialists. These results suggest that intraspecific extremes in body size for beetle species depend, in part, on the type of food resource and that this principle may apply to both temperate and tropical beetles, as well as for species collected from the same locality and sharing the same general environment (here arboreal). The data for specialist and generalist leaf-feeders also tend to support the hypothesis that high variation in size could increase the niche of the species and may have a buffering effect when food resources are unpredictable.

Keywords: Body size, Chrysomelidae, Curculionidae, feeding habits, host specificity, Papua New Guinea.

INTRODUCTION

In recent years, there has been considerable interest in body size as a determinant of the structure of animal communities. Many studies have focused on the relationship between body size and species abundance (e.g., MORSE et al., 1988; BASSET & KITCHING, 1991; STORK & BLACKBURN, 1993; TOKESHI, 1993) and many authors have tested the hypothesis that energy availability limits the abundance of organisms of different size differently (e.g., GRIFFITHS, 1992; BLACKBURN et al., 1993a). To date, the results are ambiguous (e.g., BLACKBURN et al., 1993a; BLACKBURN et al., 1993b; GASTON et al., 1993). Quite surprisingly, although the effects of energy availability (i.e., food quantity and quality) upon variation in size of a particular species have been investigated for many years (e.g., RICHARDS, 1948; PALMER, 1985), few studies considered intraspecific variation in body size and its putative relationships with community structure and, in particular, whether this variable could explain rarity or niche partitioning (e.g., GASTON & LAWTON, 1990).

In an interesting paper, ANDERSEN & NILSSEN (1983) examined the intraspecific variation in adult body size of a number of beetles in 28 families from Northern and Central Europe, determined by the ratio of maximum : minimum length observed in a population. Their data suggested that the type of food resource used by beetle larvae exert an important effect on variation in adult body size. Further, they showed that most of the variation in adult body size is often unrelated to sex, and that data extracted from the literature are usually similar to field data, providing that geographic variation is not extensive (i.e., that local races do not differ in body size). Thus, the effect of food resource on intraspecific variation in adult body size over the entire geographic range of species requires, primarily, partitioning according to, and study within, local populations, to remove any confounding effect of geographic variation.

For many tropical beetles, the information derived from museum collections appears to be unsuited for testing whether local intraspecific variation in adult body size is influenced by feeding ecology. Local collections in the tropics rarely encompass an entire year of seasonal cycle with different sampling methods appropriate to sample entire communities. Often, it is not known whether beetles foraging on vegetation feed on the plant species from which they were collected or whether they are merely transient. Frequently, knowledge of feeding specialization (i.e. specialist or generalist) is unavailable. Thus, there is a need for independent field studies in the tropics, to assess the feeding ecology of beetle species, in order to test the hypothesis, and to plan subsequent experimental studies.

A study of the local determinants of species richness and host specificity of insect herbivores associated with ten species of forest trees in Papua New Guinea (Y. BASSET, unpublished) provided the opportunity to test whether the trends reported by ANDERSEN & NILSSEN (1983) apply to tropical beetles, to beetles of close taxonomic affinity, and to beetles sharing the same general environment at a specific location. With field data obtained during one year at a single location with different sampling methods, we tested the hypothesis that local intraspecific variation in body size of arboreal leaf beetles and weevils is influenced predominantly by their feeding ecology, determined by feeding trials with adults.

MATERIAL AND METHODS

Study site and insect collecting

The study was performed on the slopes of Mt Kaindi, near and within the grounds of the Wau Ecology Institute, Wau, Papua New Guinea (7° 24' S, 146° 44' E). Collecting ranged from 1,100-2,362 m (summit) in altitude, but was mostly confined to 1,200 - 1,400 m. Mt Kaindi has been cleared locally, leaving a mosaic of grasslands and forest patches. The main forest formations encountered on the slopes include lower and mid-montane rain forest (JOHNS, 1982). The climate may be classified as "humid to perhumid mesothermal with little or no water deficit" (MCALPINE *et al.,* 1983). The study area is detailed further by GRESSITT & NADKARNI (1978).

Insects were collected from ten plant species, representing pioneer and persistent species of native forest trees and shrubs. These were: *Elmerrillia tsiampacca* (L.) DANDY (Magnoliaceae); *Cinnamomum* cf *culilaban* (L.) PRESL (Lauraceae); *Piper plagiophyllum* K. SCH. & LAUT. (Piperaceae); *Ficus nodosa* TEYS. & BINN.

(Moraceae); *Pipturus argenteus* WEDD. (Urticaceae); *Castanopsis acuminatissima* A. DC. (Fagaceae); *Caldcluvia brassii* HOOGL. (Cunioniaceae); *Aleurites moluccana* WILLD. (Euphorbiaceae); *Melicope denhamii* (SEEM.) T. HARTLEY (Rutaceae); and *Cordia dichotoma* FORST. (Boraginaceae).

Chrysomelidae and Curculionidae were collected from the foliage of the study trees during day- and night-time by hand collecting, foliage beating, branch clipping, flight-interception traps (see SPRINGATE & BASSET, in press) and pyrethrum knockdown (using the same general protocol of ALLISON *et al.*, 1993). Living specimens from the first three of these methods were used in feeding trials (see next section). Sampling was performed from February 1992 to April 1993. When the foliage could not be sampled from the ground, the single rope technique provided access to the crowns (PERRY, 1978). Sampling effort was the same for each tree species and all material thus derived has been considered for subsequent analyses.

Morphospecies assignment and assessment of ecology

Adult leaf beetles and weevils were assigned to morphospecies, on the basis of external characters, by the first author in Papua New Guinea. Since knowledge of the ecology of most Papuan beetles is fragmentary, insect specialization had to be assessed from feeding trials in the laboratory. Live adults were stored in plastic vials, at room temperature and in conditions of near-saturated relative humidity. They were provided with fresh foliage of the tree species from which they were collected, until they died or accepted food. In the latter, they were then tested in random order for 24 h periods on the foliage of the 9 other study species. Feeding damage was scored visually, relative to insect body size, on a logarithmic scale, as follows: 0: no feeding; 1: attempting to feed; 10: moderate feeding; 100: extensive feeding. This procedure emphasized regular feeding in comparison with food-probing. Insects were assigned to three leaf-feeding categories according to the results of these tests: (a) "leaf-feeder specialists", i.e., insects tested on three or more plant species but which only fed on the plant from which they were collected (sum of feeding scores < 100); (b) "leaf-feeder generalists", i.e., insects tested on three or more plant species and which fed on two or more plants, belonging to different plant families (sum of feeding scores ≥ 100); and (c) "leaf-feeder, unknown degree of specialization", i.e., insects which, because of death, could not be tested on more than two plant species. The advantages and limitations of this procedure are discussed further in BASSET (1994). In general, there was a good correspondence between the food preferences as assesed in feeding trials and insect presence in particular tree species.

Further, weevil morphospecies which did not feed in the trials, or which were collected dead (i.e., by flight-interception traps or pyrethrum knockdown) were assigned to the categories "leaf-feeder, unknown" or "wood-borer" using information provided by experienced weevil taxonomists (E. C. ZIMMERMAN & R. S. ANDERSON, pers. comm.) and the relevant literature (e.g., ANDERSON, in press).

All weevil and leaf beetle material was later dry mounted at the Bishop Museum, Honolulu. Morphospecies assignment was checked and updated by the third author. Some of the curculionids had been identified by R. T. THOMPSON and E. C. ZIMMERMAN. Since specific names were not available for many of the morphospecies collected, these were assigned species numbers (see Appendix). The material has been deposited in the collections of the Bishop Museum.

Measurement of body size

For the analyses, we selected morphospecies of which at least 10 individuals were available. The 3 shortest and 3 longest individuals from each morphospecies were selected by visual examination and measured, with the intention of using the least and greatest dimensions obtained in subsequent analyses. For some morphospecies where the extremes were not evident from visual inspection, the number of individuals measured was greater. Measurements were taken by the second author, using an eyepiece micrometer at magnifications of 7x, 10x, 20x and 30x, dependent upon the size of the specimen. Body length was considered to be the sum of the lengths, along a mid-line, of the head (in anterior view), pronotum and elytron, excluding appendages. Head length was estimated from the occiput to the anterior margin of the labrum (Chrysomelidae) or from the occiput to a tangent linking the lower margin of the eyes (Curculionidae). Lengths were recorded to the nearest 0.1 mm. Sexes were not distinguished for measurements and subsequent analyses.

Variables derived from measurements and statistical methods

From our measurements, we derived the ratio of the maximum : minimum lengths (hereafter termed "size variation index") and the mean length [(maximum + minimum lengths)/2] for each morphospecies. We prefer to report intraspecific variation in body size as a simple ratio based on range, rather than as a measurement of deviation from central tendency (i.e., standard error, standard deviation) for the following reasons: (a) our procedure emphasizes extremes of body sizes within the local populations collected, which may be related to extremes in food quality, rather than average values and variations; (b) our measurements can be obtained rapidly and compared readily with the available literature, which rarely report measurements of deviation from central tendency (see ANDERSEN & NILSSEN, 1983); and (c) reporting the latter for untransformed variables with skewed, non-normal, distributions, such as body lengths, is inappropriate.

After log-transforming the variables (in natural base), all, with the exception of the number of individuals available for analyses, satisfied the assumption of normality (Kolmogorov-Smirnov-Lliefors tests, $p > 0.05$). Therefore, we used parametric statistics with transformed values for analyses involving all but the latter variable. We performed analyses of variances (ANOVA) with the size variation index as the dependent variable and the following grouping variables: (a) feeding categories (1 = specialists, 2 = generalists, 3 = leaf-feeders, unknown, 4 = wood-borers); (b) classes of mean body size (1 = 0.1 - 3.5 mm, 2 = 3.6 - 6.5 mm, 3 = 6.6 - 9.5 mm, 4 = > 9.5 mm); (c) taxonomic categories of leaf-feeders (1 = Eumolpinae, 2 = Galerucinae, 3 = Entiminae, 4 = Tychiinae); and (d) classes of abundances (1 = 10 - 15 individuals available for analyses, 2 = 16 - 25, 3 = 26 - 50, 4 = > 50). As a more powerful analysis, we further tested for differences in the slopes of the regressions on the minimum and maximum lengths measured within the different feeding categories of beetles. Since both maximum and minimum lengths are subject to measurement error, we prefer to use the reduced major axis method (RMA; SOKAL & ROHLF, 1981) over ordinary least squares for this purpose (see further discussion in MCARDLE, 1988). Since debate continues upon which statistic should be used to compare two RMA slopes (e.g., IMBRIE, 1956; CLARKE, 1980; MCARDLE, 1988), only the 95% confidence limits of the slopes are reported. For this purpose, we used the equation of JOLICOEUR & MOSIMANN (1968) instead of the equation pro-

posed by CLARKE (1980), since only the former performs well with low sample size such as ours (see the simulations of McARDLE, 1988; Table 1).

Also, we performed similar analyses using body weight instead of body length. For these, the minimum and maximum morphospecies biomass was estimated from regressions on body length (mm) and insect biomass (g dry weight) computed by SCHOENER (1980) for tropical rainforest beetles.

RESULTS

In total, using all collecting methods, 134 and 208 morphospecies, representing 2,183 and 2,084 individuals, of Chrysomelidae and Curculionidae, respectively, were collected on the foliage of the 10 tree species studied at Wau. Of this material, 33 and 39 morphospecies, represented by 1490 and 1299 individuals, of Chrysomelidae and Curculionidae, respectively, were selected for analyses (i.e., at least 10 individuals were available for each morphospecies). The identity, if known, the measurements of body lengths, the size variation index and the feeding ecology of each of these morphospecies are detailed in the Appendix. Many of the selected morphospecies of weevils (64 %) were leaf-feeders. However, many more morphospecies of wood-borers were present at low frequency in our samples and could not be considered in the present analyses. In addition, 59 % of leaf-feeding morphospecies selected for the analyses (23 of 39) were specialists. Most of the selected leaf-feeders belonged to the subfamilies Eumolpinae, Galerucinae, Entiminae and Tychiinae, whereas most wood-boring morphospecies belonged to Cryptorhynchinae and Zygopinae (see Appendix).

All analyses detailed below were performed with a variation index expressed as either body size or body weight. Since statistical trends were similar for both variables, we do not present results pertaining to the index of variation in body weight and omit this variable from the discussion.

First, preliminary analyses showed a positive correlation between the mean length measured and the ratio of maximum : minimum lengths (Fig. 1a; Pearson's correlation coefficient r = 0.390, p < 0.01). This suggests that putative differences in the size variation index can result from differences in body size per se (i.e., related to phylogeny) or from methodological problems in body size measurement (i.e., the measurement error may be different between large and small morphospecies). We also noted, that there was no significant difference in the body size of leaf-feeders and of wood-borers (t-test, t = 1.05, p = 0.306). However, for leaf-feeders, specialists were significantly smaller than generalists (t = 2.50, p < 0.05).

Second, we observed a significant positive correlation between the number of individuals available for analyses and the size variation index (Fig. 1b; Spearman rank correlation coefficient r_s = 0.346, p < 0.01). Since the number of individuals available reflects to some extent the abundance of a particular morphospecies in the field, it suggests that morphospecies with high population levels exhibit more variation in body size. There was no significant difference between the number of individuals in the leaf-feeding and wood-boring categories (Mann-Whitney U = 450.5, p = 0.526), nor in the number of individuals in the specialist and generalist categories (U = 139.0, p = 0.198).

The distribution of the size variation index, according to feeding category, is summarized in Tab. 1. The mean of the index increased in the sequence: specialists - generalists - wood-borers. Since it is probable that the "unknown" category of leaf-feeders included both specialists and generalists, the mean of the index (as reported for transformed data) appears intermediate between those of both.
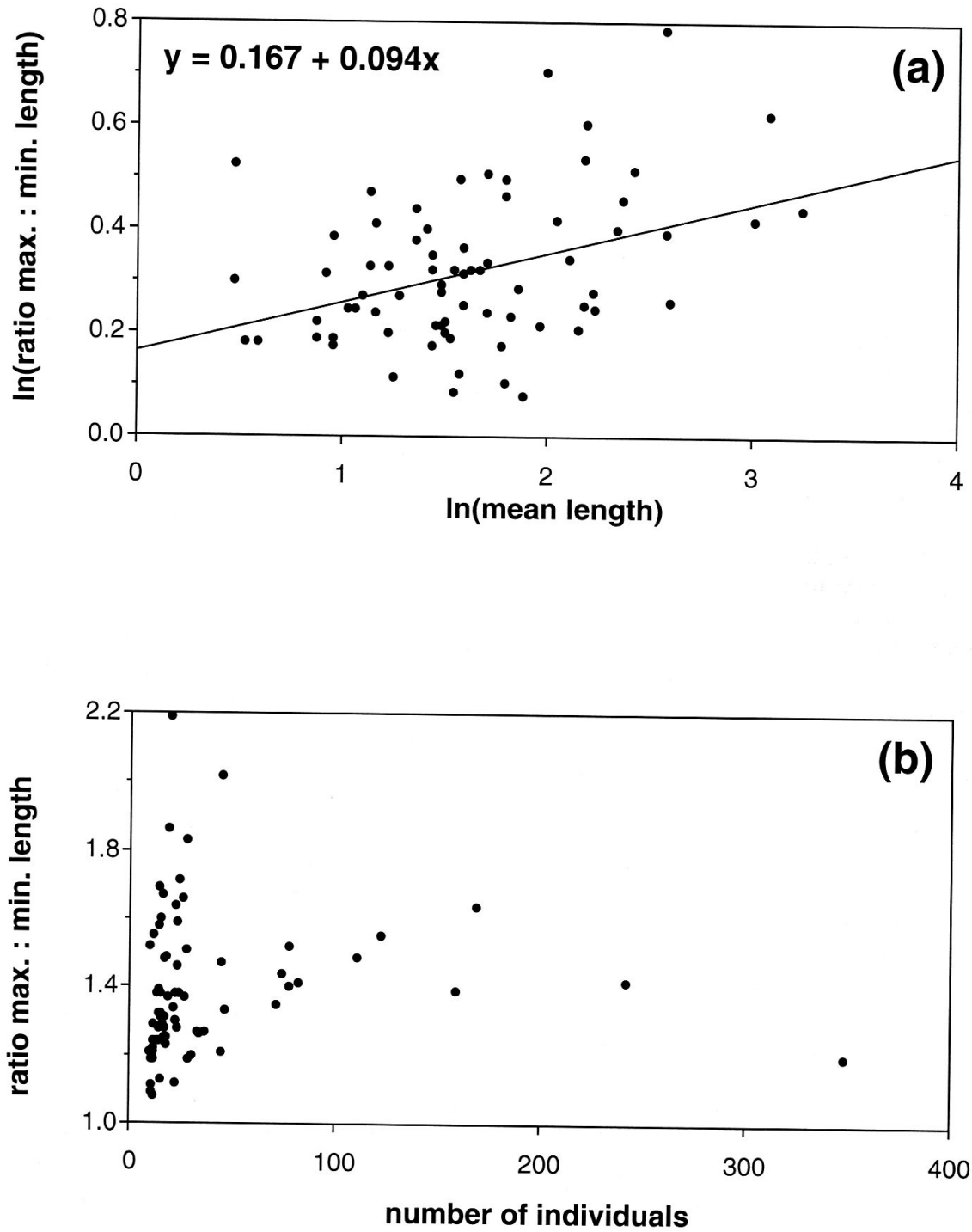
Fig. 1. Scatter plots of (a) log-transformed mean body length of morphospecies against log-transformed ratio of maximum : minimum lengths measured; and (b) number of individuals available for the analyses against ratio of maximum : minimum lengths.

Tab. 1. Summary of statistics for the distribution of the size variation index according to feeding category (no. of morphospecies, minimum, maximum and median of untransformed data, and mean of transformed data).

Category	n	Min.	Max.	Median	Mean ± s.e.
Leaf-feeders - specialists	23	1.08	1.64	1.280	0.248 ± 0.020
Leaf-feeders - generalists	16	1.24	2.02	1.405	0.370 ± 0.032
Leaf-feeders - unknown	19	1.09	1.69	1.250	0.283 ± 0.031
Wood-borers	14	1.22	2.19	1.550	0.434 ± 0.041

When all morphospecies were considered, the size variation index was related significantly to feeding category (ANOVA, Tab. 2). In particular, the index differed significantly between leaf-feeders and wood-borers ($t = 3.19$, $p < 0.01$), and between specialist and generalist leaf-feeders (Tab. 2). Removing the ill-defined category "leaf-feeders, unknown" (which included both specialists and generalists), resulted in increasing the significance of feeding habit. To a lesser extent, the index was influenced significantly by body size per se (Tab. 2), and even less so by the number of individuals available for the analyses. However, it is probable that the ultimate F-values of these ANOVAs depend on the categories of grouping variables considered for the analyses. When the ANOVAs were restricted to leaf-feeders, as a specific test of the influence of taxonomy, the effect of feeding ecology on the size variation index was significant, whereas those of body size, abundance and taxonomic category were not (Tab. 2). Overall, the various ANOVAs performed suggest that feeding category exerted a more significant influence on the size variation index than body size per se, abundance or taxonomic category.

Next we considered either leaf beetles or weevils. In leaf beetles, the size variation index was significantly lower in specialists than in generalists ($t = 2.33$, $p < 0.05$) but not the mean body length ($t = 0.41$, $p = 0.685$). In weevils, both the size variation index and mean body length were significantly lower in specialists than in generalists ($t = 2.76$, $p < 0.05$ and $t = 2.73$, $p < 0.05$, respectively). Although these analyses within insect families involve low sample sizes, they suggest that differences in the size variation index are unlikely to be due solely to taxonomic category. Further, in the case of leaf beetles, they also suggest that the size variation index vary more significantly than body size when specialist and generalist categories are compared.

We regressed the minimum against the maximum lengths measured within feeding categories to minimize the effect of body size per se and computed RMA regressions for specialists, generalist and wood-borers (Fig. 2). Whereas the slope of the subset of specialist leaf-feeder data appeared not to differ from than that of generalists (when the 95% confidence limits of both slopes in Fig. 2 are compared), that of the wood-borer data subset was significantly higher than that of specialist leaf-feeders. These trends were similar using ordinary least squares regressions (i.e., slope for specialists = 0.927, 95% confidence limits = 0.881 and 0.972; slope for wood-borers = 1.230, confidence limits = 1.164 and 1.297; t-test for the equality of slopes $t = 3.87$, $p < 0.001$). These results suggest that feeding category, rather than body size per se, exerted greater influence on the size variation index.

Tab. 2. Results of one-way ANOVA with transformed size variation index as the dependent variable and feeding category, classes of abundance, classes of body size and insect subfamilies as grouping variables (see text). Models are listed in order of decreasing significance.

Model	MS	MS error	df	F-ratio	p
a) all morphospecies:					
Index * feeding ecology [1]	0.165	0.015	2, 50	11.05	0.001
Index * feeding ecology	0.122	0.016	3, 68	7.66	0.001
Index * body size	0.098	0.017	3, 68	5.73	0.001
Index * abundance	0.050	0.019	3, 68	2.60	0.059
b) leaf-feeders only:					
Index * feeding ecology [2]	-	-	-	3.42	0.002
Index * feeding ecology	0.071	0.014	2, 55	5.01	0.010
Index * body size	0.038	0.015	3, 54	2.54	0.066
Index * abundance	0.037	0.015	3, 54	2.45	0.073
Index * taxonomy	0.038	0.016	3, 43	2.44	0.077

[1] Analyses without the leaf-feeder category "unknown"
[2] Analyses without the leaf-feeder category "unknown". In this case the statistic used is a t-test.

DISCUSSION

Our analyses suggest that the type of feeding habit, the body size per se (i.e., large species are more likely to exhibit a wide range of body size) and, to a lesser extent, the number of individuals available for analyses (i.e., species with high abundance are more likely to exhibit high range of body size) influence the local intraspecific range of body size in leaf beetles and weevils. Within these families, in particular leaf-feeders, the influence of taxonomic category at the subfamily level appears less obvious. Both the analyses of variance and the reduced major axis regressions suggest that the influence of feeding category on the size variation index is more important than that of body size per se. To some extent, this interaction between body size, range of body size and feeding ecology might be anticipated since polyphagous insect species are often (but not always) larger than specialists (e.g., GASTON & LAWTON, 1988; GASTON & REAVEY, 1989), and this is confirmed by our data. It is possible that the positive correlation between the number of individuals available for analysis and the size variation index may be the result of our measurements being unrepresentative of the body range within the populations studied (i.e., if our sample sizes were too small to represent the true variation in body size). However, inspection of Fig. 1b shows that the situation is certainly more complex than this, with many morphospecies with low population levels showing high variation in body size. Furthermore, the data points appear to cluster into different subgroups. Therefore, the contribution of the number of individuals available for analysis to variation in body size is weak and ambiguous, as suggested by the ANOVA's. In addition, sexual dimorphism may influence overall patterns in intraspecific range of body size for beetles, but the effects of this factor were shown to be negligible by ANDERSEN & NILSSEN (1983).
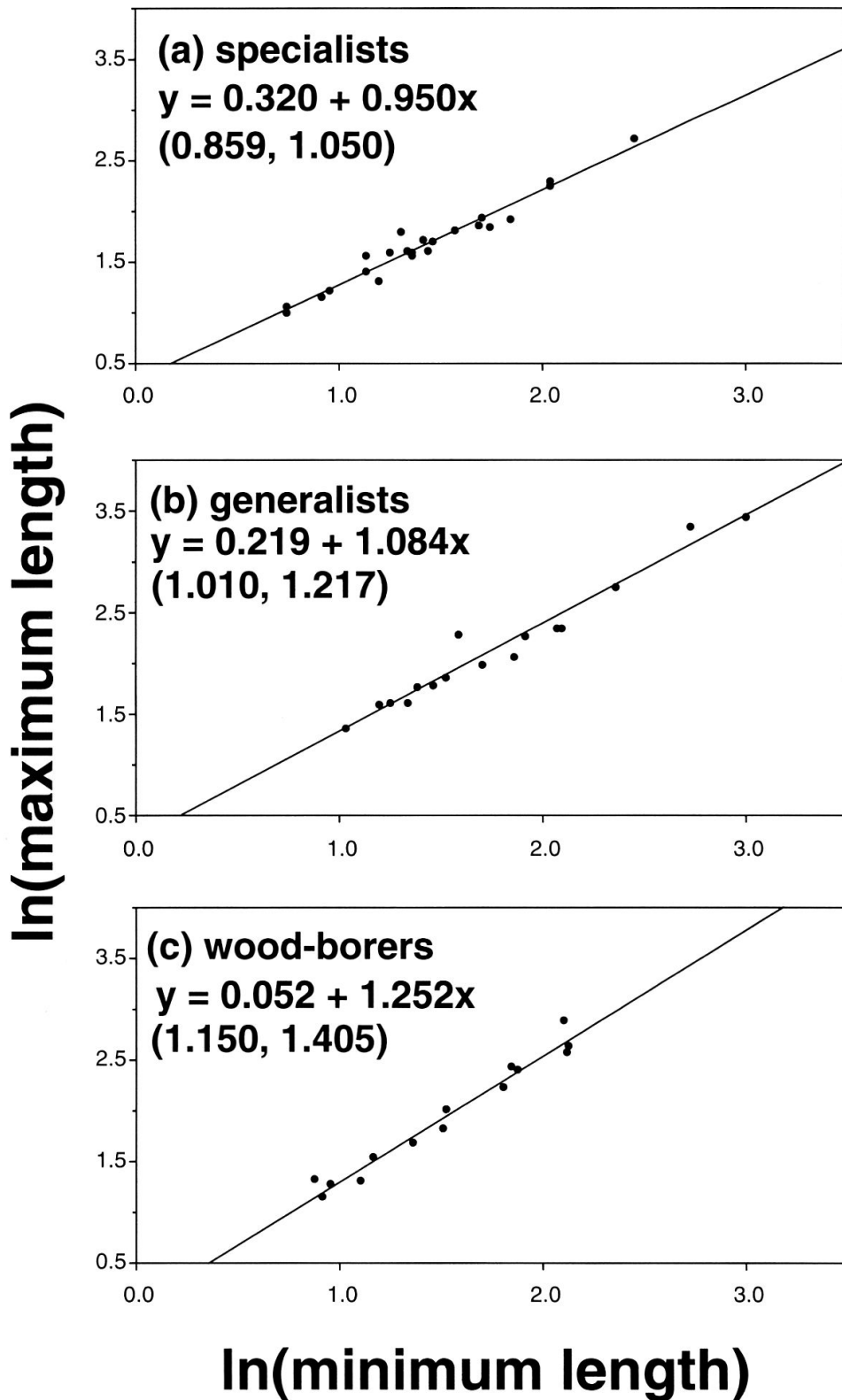
Fig. 2. Scatter plots of the minimum length against the maximum length measured for (a) specialist leaf-feeders; (b) generalist leaf-feeders; and (c) wood-borers. Lines indicate the regressions as calculated by the method of the reduced major axis with, in brackets, the 95% confidence limits as calculated using the equation of JOLICOEUR & MOSIMANN (1968).

It is most probable that our data support the contention of ANDERSEN & NILSSEN (1983) that the range of body size in beetles is in part influenced by the feeding habits. These authors did not test for a possible influence of body size per se and phylogeny and, thus, our analyses are more robust and suggest that this observation may indeed apply to both temperate and tropical beetles. Furthermore, our data set suggests that this principle may apply to species of close taxonomic affinity, collected from the same locality and sharing the same general environment, in the present study, leaf beetles and weevils foraging within the foliage of trees at Wau.

From their results, ANDERSEN & NILSSEN (1983) suggested that beetles with free-living larvae have, in general, lower intraspecific variation than beetles with wood-boring and parasitoid larvae since high intraspecific variation in size is common in species whose larvae are unable to choose and determine their own nutritional situation. They reasoned that (a) usually, free-living larvae experience rather uniform conditions and if extreme conditions occur, they do not complete their development rather than emerging as small adults; and (b) it is probable that a high variation in size increases the niche of the species and has a buffering effect in unpredictable environments (or when the species depends on unpredictable food resources). Although our sample size was low, the differences observed between specialist and generalist leaf-feeders lend support to (b) (see further discussions in HESPENHEIDE, 1973 and WASSERMAN & MITTER, 1978, for example). This situation may be particularly relevant when extremes in food quality are encountered by the ovipositing adult (e.g., for wood-borers and generalist leaf-feeders). Thus, an index reporting intraspecific extremes in body size may be as useful, if not more so, than a measurement of deviation from central tendency. Using body weights instead of body lengths did not alter the interpretation of the results. The discussion whether a population contains a variety of phenotypes with genetically fixed size, or whether each individual is flexible with the possibility of becoming large or small (see ANDERSEN & NILSSEN, 1983), is beyond the scope of the present paper.

We believe that differences in the size variation index between wood-borers and leaf-feeders might have been even more significant, had our wood-borers been obtained from dying major branches and trunks, or logs and stumps, instead of the foliage of living trees. It is possible that a high proportion of the wood-borers we examined breed in smaller, rather than major, branches. As such, these species may be smaller (e.g., HESPENHEIDE, 1969; GRESSITT & SAMUELSON, 1981) and their breeding environment may be less durable and/or less buffered (i.e., against desiccation) than in larger branches and logs. This may result in greater larval mortality and a lower probability of the emergence of small adults.

Our assignments to feeding categories, particularly for leaf-feeders, pertained to adult beetles, not to larvae. It is possible that some seed- and flower-eating weevils may have been classified wrongly as wood-borers and leaf-feeders, respectively, and some wood-boring weevils, which fed on foliage, may have been classified wrongly as leaf-feeders. A better assignment might have increased differences in the size variation index between feeding categories. However, one point remains intriguing. Very few free-living larvae of leaf beetles and weevils were observed on the foliage of the study trees. It is probable that most of the larvae of the morphospecies collected are root-feeders or concealed feeders in plant tissues. For example, in the tropics leaf-feeding adults of Entimini (e.g., GRESSITT & HORNABROOK, 1985, as Leptopiinae), Pachyrhynchini (GRESSITT, 1966, as Brachyderinae) and Eumolpinae (e.g., JOLIVET, 1988) are often root-feeders as larvae, whereas leaf-feeding adults

356

of Baridinae may be concealed feeders in the larval stage (e.g., MARQUIS, 1991). If our observations about the extremes of variation in body size for arboreal leaf beetles and weevils at Wau are accurate and can be generalized for other locations and environments, this would further suggest that tropical beetle species which are root-feeders and leaf-feeders as larvae and adults, respectively, may be restricted to either the generalist or the specialist habits during both the larval and adult stages. Indeed, JOLIVET (1992) indicates that examples of "temporary oligophagy" (i.e., a switch to a different breadth of diet during different development stages) are difficult to find among Coleoptera. This may be particularly relevant to leaf-feeding adults. There are species of Galerucinae which are relatively specialized as root-feeders in the larval stages but rather generalist as pollen-eating adults (FERGUSON & METCALF, 1985; SAMUELSON, 1994). There is a requirement for greater investment into research upon the life history, ecology and taxonomy of herbivorous beetles in the tropics, in order to test the above suggestion.

ACKNOWLEDGMENTS

RÉSUMÉ

L'ampleur de la variation de la taille du corps et le régime alimentaire: une étude en Papouasie Nouvelle-Guinée avec des chrysomèles et charançons arboricoles (Coleoptera: Chrysomelidae, Curculionidae). - Nous avons mesuré l'ampleur de la variation intraspécifique de la taille du corps (définie comme le quotient des longueurs maximum : minimum mesurées dans une population d'au moins 10 individus) de respectivement 33 et 39 morpho-espèces de Chrysomelidae et Curculionidae, qui ont été récoltées à l'aide de diverses méthodes sur le feuillage de 10 espèces d'arbres provenant d'une même localité, près de Wau, en Papouasie Nouvelle-Guinée. Les adultes vivants ont été testés sur le feuillage des arbres étudiés, afin de les assigner à l'une des quatre catégories suivantes: (1) défoliateur, spécialiste; (2) défoliateur, généraliste; (3) défoliateur, incertain; et (4) xylophage. Nos analyses suggèrent que le type de régime alimentaire influence de manière prédominante l'ampleur de la variation de la taille du corps, alors que les effets de la taille du corps en soi, du nombre d'individus disponibles pour les analyses et des différentes catégories taxonomiques considérées sont moins évidents ou absents. En général, l' ampleur de la variation de la taille du corps est plus élevée pour les xylophages que pour les défoliateurs, et, de même, celle des généralistes est plus élevée que celle des spécialistes. En particulier, la pente de regression des longueurs minimum contre maximum calculées par la méthode de l'axe majeur réduit est significativement plus élevée dans le cas des xylophages que dans le cas des spécialistes. Ces résultats suggèrent que les extrêmes de taille interspécifiques dépendent en partie du type de resource alimentaire et que cette loi pourrait s'appliquer pour les coléoptères des régions tempérées comme tropicales, comme pour des espèces récoltées d'une même localité et dépendant d'un même milieu général (en l'occurence ici, le milieu arboricole). Les données pour les spécialistes et généralistes tendent aussi à confirmer l'hypothèse qu'une variation de taille élevée puisse élargir la niche d'une espèce et puisse avoir un effet tampon lorsque les resources alimentaires utilisées sont difficiles à prévoir.

REFERENCES

ALLISON, A., SAMUELSON, G. A. & MILLER, S. E. 1993. Patterns of beetle species diversity in New Guinea rain forest as revealed by canopy fogging: preliminary findings. *Selbyana 14:* 16-20.

ANDERSEN, J. & NILSSEN, A. C. 1983. Intrapopulation size variation of free-living and tree-boring Coleoptera. *Can. Ent. 115:* 1453-1464.

ANDERSON, R. S. in press. An evolutionary perspective on diversity in Curculionoidea. *In:* ANDERSON, R. S. & LYAL, C. H. C. (eds) *Biology and Phylogeny of Curculionoidea: Proceedings of a Sym-*

posium convened at the XVIII International Congress of Entomology, July 1988. Mem. Ent. Soc.Washington.

BASSET, Y. 1994. Palatability of tree foliage to chewing insects: a comparison between a temperate and a tropical site. *Acta Oecologica 15:* 181-191.

BASSET, Y. & KITCHING, R. L. 1991. Species number, species abundance and body length of arboreal arthropods associated with an Australian rainforest tree. *Ecol. Entomol. 16:* 391-402.

BLACKBURN, T. M., BROWN, V. K., DOUBE, B. M., GREENWOOD, J. J. D., LAWTON, J. H. & STORK, N. E. 1993a. The relationship between abundance and body size in natural animal assemblages. *J. Anim. Ecol. 62:* 519-528.

BLACKBURN, T. M., LAWTON, J. H. & PIMM, S. L. 1993b. Non-metabolic explanations for the relationship between body size and animal abundance. *J. Anim. Ecol. 62:* 694-702.

CLARKE, M. R. B. 1980. The reduced major axis of a bivariate sample. *Biometrika 67:* 441-446.

FERGUSON, J. E. & METCALF, R. L. 1985. Cucurbitacins. Plant-derived defense compounds for *Diabroticites. J. Chem. Ecol. 11:* 311-318.

GASTON, K. J., BLACKBURN, T. M. & LAWTON, J. H. 1993. Comparing animals and automobiles: a vehicle for understanding body size and abundance relationships in species assemblages? *Oikos 66:* 172-179.

GASTON, K. J. & LAWTON, J. H. 1988. Patterns in body size, population dynamics and regional distribution of bracken herbivores. *Am. Nat. 132:* 662-680.

GASTON, K. J. & LAWTON, J. H. 1990. The population ecology of rare species. *J. Fish Biol. 37 (Suppl. A):* 97-104.

GASTON, K. J. & REAVEY, D. 1989. Patterns in the life histories and feeding strategies of British macrolepidoptera. *Biol. J. Linn. Soc. 37:* 367-381.

GRESSITT, J. L. 1966. The weevil genus *Panthorhytes* (Coleoptera), involving cacao pests and epizoic symbiosis with cryptogamic plants and microfauna. *Pac. Ins. 8:* 915-965.

GRESSITT, J. L. & HORNABROOK, R. W. 1985. *Handbook of Common New Guinea Beetles.* 2nd ed. Wau Ecology Institute (Handbook no. 2), Wau, 87 pp.

GRESSITT, J. L. & NADKARNI, N. 1978. *Guide to Mt. Kaindi. Background to montane New Guinea Ecology.* Wau Ecology Institute (Handbook no. 5), Wau, 135 pp.

GRESSITT, J. L. & SAMUELSON, G. A. 1981. Structural variation of organism groups studied in the Kilauea forest. Cerambycid tree borers. *US / IBP Synthesis Series 15:* 288-290.

GRIFFITHS, D. 1992. Size, abundance, and energy use in communities. *J. Anim. Ecol. 61:* 307-315.

HESPENHEIDE, H. A. 1969. Larval feeding sites of species of *Agrilus* (Coleoptera) using a common host plant. *Oikos 20:* 558-561.

HESPENHEIDE, H. A. 1973. Ecological inferences from morphological data. *Ann. Rev. Ecol. Syst. 4:* 213-229.

IMBRIE, J. 1956. Biometrical methods in the study of invertebrate fossils. *Bull. Am. Mus. Nat. Hist. 108:* 215-252.

JOHNS, R.B. 1982. Plant zonation. *In:* GRESSITT, J.L. (ed.) *Biogeography and Ecology of New Guinea,* pp. 309-330. W. Junk, The Hague.

JOLICOEUR, P. & MOSIMANN, J. E. 1968. Intervalles de confiance pour la pente de l'axe majeur d'une distribution normale bidimensionelle. *Biométrie-Praximétrie 9:* 121-140.

JOLIVET, P. 1988. Food habits and food selection of Chrysomelidae. Bionomic and evolutionary perspectives. *In:* JOLIVET, P., PETITIPIERRE, E. & TSIAO, T. H. (eds) *Biology of Chrysomelidae,* pp. 1-24. Kluwer Academic Publisher, Dordrecht.

JOLIVET, P. 1992. *Insects and Plants. Parallel Evolution and Adaptations.* 2nd ed. Sandhill Crane Press Inc., Gainesville, Florida, 190 pp.

MARQUIS, R. J. 1991. Herbivore fauna of *Piper* (Piperaceae) in a Costa Rican wet forest: diversity, specificity and impact. *In:* PRICE, P. W., LEWINSOHN, T. M., FERNANDES, G. W. & BENSON, W. W. (eds) *Plant-Animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions,* pp. 179-208. John Wiley, New York, 639 pp.

MCALPINE, J. R., KEIG, G. & FALLS, R. 1983. *Climate of Papua New Guinea.* CSIRO, Canberra, 200 pp.

MCARDLE, B. H. 1988. The structural relationship: regression in biology. *Can. J. Zool. 66:* 2329-2339.

MORSE, D. R., STORK, N. E. & LAWTON, J. H. 1988. Species number, species abundance and body length relationships of arboreal beetles in Bornean lowland rain forest trees. *Ecol. Entomol. 13:* 25-37.

PALMER, J. O. 1985. Life-history consequences of body-size variation in the milkweed leaf beetle, *Labidomera clivicollis* (Coleoptera: Chrysomelidae). *Ann. Ent. Soc. Am. 78:* 603-608.

PERRY, D. R. 1978. A method of access into the crowns of emergent and canopy trees. *Biotropica 10:* 155-157.

RICHARDS, O. W. 1948. The interaction of environmental and genetic factors in determining the weight of grain weevils, *Calandra granaria* (L.) (Col. Curculionidae). *Proc. zool. Soc. Lond. 118:* 49-81.

SAMUELSON, G. A. 1994. Pollen consumption and digestion by leaf beetles. *In:* P. H. JOLIVET, L. COX

& E. PETITPIERRE (eds) *Novel aspects of the Biology of Chrysomelidae*, pp. 179-183, Kluwer, Dordrecht, 582 pp.

SCHOENER, T. W. 1980. Length-weight regressions in tropical and temperate forest-understorey insects. *Ann. Ent. Soc. Am. 73:* 106-109.

SOKAL, R. R. & ROHLF, F. J. 1981. *Biometry.* Freeman, New York, 859 pp.

STORK, N. E. & BLACKBURN, T. M. 1993. Abundance, body size and biomass of arthropods in tropical forest. *Oikos 67:* 483-489.

SPRINGATE, N. D. & BASSET, Y. in press. Diel activity of arboreal arthropods associated with Papua New Guinean trees. *J. nat. Hist.*

TOKESHI, M. 1993. Species abundance patterns and community structure. *Adv. Ecol. Res. 24:* 111-186.

WASSERMAN, S. S. & MITTER, C. 1978. The relationship of body size to breadth of diet in some Lepidoptera. *Ecol. Entomol. 3:* 155-160.

Appendix. Identity (if known) of the morphospecies considered for analyses; smallest (S) and largest (L) lengths measured (mm); ratio maximum : minimum lengths; feeding ecology (LF = leaf feeeder, WB = wood-borer; sp = specialist; ge = generalist; un = unknown) and number of individuals available for analyses.

Taxa	S	L	Ratio	Ecology [1]	n
Chrysomelidae					
Cryptocephalinae					
Coenobius sp.	2.2	2.7	1.21	LF - un	10
Eumolpinae					
Rhyparida coriacea JACOBY	7.9	10.5	1.32	LF - ge	14
Rhyparida sp. *(bryanti* group)	8.3	12.4	1.49	LF - un	18
Rhyparida sp.	4.8	6.1	1.27	LF - sp	33
Rhyparida sp.	5.7	6.3	1.11	LF - sp	11
Rhyparidella wauensis GRESSITT	3.3	4.9	1.49	LF - ge	111
Rhyparidella? sp.	3.7	6.0	1.64	LF - sp	169
Rhyparidella? sp.	3.5	5.0	1.42	LF - ge	242
Rhyparidella? sp.	2.8	3.9	1.39	LF - ge	159
Rhyparidella? sp.	4.6	6.4	1.40	LF - ge	78
Rhyparidella? sp.	5.5	7.3	1.33	LF - ge	46
Rhyparidella? sp.	3.3	3.7	1.12	LF - sp	22
Rhyparidella? sp.	3.8	5.0	1.32	LF - sp	15
Rhyparidella? sp.	3.9	4.8	1.24	LF - sp	12
Rhyparidella? sp.	3.8	5.0	1.34	LF - ge	21
Stethotes integra BALY	5.4	6.4	1.19	LF - sp	29
Stethotes suturalis BRYANT	3.1	4.1	1.31	LF - sp	17
Stethotes nr *lateralis* BALY	4.1	5.6	1.37	LF - sp	27
Stethotes ?nigritula BALY	2.5	3.8	1.51	LF - un	28
Thyrasia? sp.	4.7	7.4	1.59	LF - un	23
Galerucinae					
Atysa sp.	7.7	9.5	1.23	LF - sp	18
Cassena sp.	4.1	6.8	1.66	LF - un	25
Momaea? sp.	3.9	4.9	1.24	LF - sp	14
Monolepta? sp.	4.5	5.1	1.13	LF - un	15
Neolepta? sp.	2.1	2.7	1.25	LF - sp	17
Neolepta? sp.	2.3	2.8	1.19	LF - un	11
Neolepta? sp.	4.0	5.0	1.25	LF - un	18
Neolepta? sp.	4.5	5.0	1.09	LF - un	11
Oides sp.	11.6	15.1	1.30	LF - sp	22
Alticinae					
Aphthonomorpha sp.	2.8	3.6	1.27	LF - un	37
Crepidodera sp.	3.1	4.8	1.55	LF - sp	122
Manobia sp.	2.1	2.9	1.37	LF - sp	19
Xenidea sp.	4.2	5.0	1.21	LF - sp	45
Curculionidae					
Apioninae					
Sp. 1	3.8	4.5	1.19	LF - un	12
Entiminae					
Apirocalus ?ebrius FAUST	6.8	9.6	1.41	LF - ge	82
Gymnopholus interpres HELLER	16.1	24.5	1.52	LF - un	10
Gymnopholus marquardti HELLER	15.3	28.4	1.86	LF - ge	19
Gymnopholus weiskei HELLER	20.1	31.1	1.55	LF - ge	12
Hellerhinus papuanus (HELLER)	8.1	10.4	1.28	LF - ge	17
Myllocerus sp.	3.5	4.9	1.38	LF - sp	22
Pantorhytes pilosus HELLER	10.6	15.7	1.48	LF - ge	17
Sp. 2	4.3	5.9	1.38	LF - ge	15
Sp. 3	4.9	9.8	2.02	LF - ge	45
Sp. 4	4.0	5.8	1.44	LF - ge	74
Sp. 5	5.5	6.9	1.26	LF - sp	34
Sp. 6	6.4	7.9	1.24	LF - ge	13

Vitticinae					
Viticis sp.	2.5	3.2	1.28	LF - sp	23
Molytinae					
Paepalophorus frontalis PASCOE	7.7	9.9	1.29	LF - sp	16
Sp. 7	4.1	5.0	1.22	LF - un	12
Sp. 8	8.3	13.2	1.58	WB	14
Sp. 9	8.2	18.0	2.19	WB	20
Sp. 10	6.1	9.3	1.52	WB	78
Cryptorhynchinae					
Sp. 11	8.4	14.0	1.67	WB	16
Sp. 12	6.3	11.5	1.83	WB	28
Sp. 13	6.5	11.1	1.71	WB	24
Sp. 14	3.9	5.4	1.38	WB	24
Sp. 15	3.0	3.7	1.22	WB	12
Sp. 16	4.6	7.5	1.64	WB	22
Sp. 17	6.3	6.8	1.08	LF - sp	12
Sp. 18	3.2	4.7	1.46	WB	23
Sp. 19	2.5	3.2	1.28	WB	14
Zygopinae					
Sp. 20	4.5	6.2	1.38	WB	13
Sp. 21	2.6	3.6	1.39	WB	14
Sp. 22	2.4	3.8	1.60	WB	15
Baridinae					
Sp. 23	4.3	5.5	1.29	LF - sp	12
Tychiinae (1)					
Sp. 24	2.6	3.4	1.31	LF - sp	15
Sp. 25	2.4	2.9	1.21	LF - un	12
Sp. 26	2.1	3.1	1.47	LF - un	45
Sp. 27	1.5	1.8	1.20	LF - un	348
Sp. 28	1.3	1.8	1.35	LF - un	71
Sp. 29	1.2	2.0	1.69	LF - un	14
Sp. 30	1.6	2.0	1.20	LF - un	30

[1] Some morphospecies may be feeding on flowers.