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ZOPHOBAS ATRATUS (FAB.) AND *Z. RUGIPES* KIRSCH
(COLEOPTERA: TENEBRIONIDAE)
ARE THE SAME SPECIES

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ABSTRACT

Morphometry of key characters and cross-breeding were used to test whether *Zophobas atratus* (Fab.) and *Z. rugipes* Kirsch might be a single species. Morphometry readily distinguished two distinct types, but substantial reproductive compatibility between them indicated that they are probably morphs of a single species. Between-population hybrids were intermediate in the measured characters. The factors maintaining the morphological differences are unknown.

Zophobas atratus (Fab.) [= *Z. morio* (Fab.)] and *Z. rugipes* Kirsch are widespread species of tenebrionids throughout Central America, parts of South America and much of the West Indies and Mexico. Distinguishing the two species has been difficult in the past because most of the differences are shape characters that vary only in degree (Table 1, Spilman, pers. comm.).

From the little information available, the species are quite similar in their habits. Both are found in bat guano and other organic litter, where they may occur in very large numbers. They have also been collected under the bark of dead trees.

I have carried out laboratory studies on the role of crowding in the biology of *Z. rugipes* for many years (Tschinkel and Willson 1971; Tschinkel and Van Belle 1976; Tschinkel 1978) and more recently I have completed field work on a population identified as *Z. atratus* (Tschinkel 1981). Because the biology and morphology of these two species seems so similar, I felt that I might be dealing with a single, rather variable, species. I therefore undertook cross-breeding experiments and a morphometric analysis of the two main characters used to distinguish the species—curvature of the male protibia, and basal angle of the penultimate antennal segment.

MATERIAL AND METHODS

COLLECTION LOCALITIES. Live specimens of *Zophobas* were collected from bat guano at the following localities: 1) cave 2 km west of Heredia, Costa Rica, July 1965; 2) bat cave, El Taladro, Dto. Comayagua, Honduras, January 1979; 3) Cueva Vieja, vicinity La Paz, Dto. La Paz, Honduras, January 1979; 4) attic of Escuela Panamericana de Agricultores, El Zamorano, Dto. Francisco Morazan, Honduras, August 1979; 5) abandoned building, Simla Station, Asa Wright Nature Center, Trinidad, November 1979.

All beetles were identified by T. Spilman as *Z. rugipes* except those from El Zamorano which were identified as *Z. atratus*. Larvae and adults were reared in the laboratory in boxes of bran and cricket feed, and were watered 3 times a week (Tschinkel and Willson 1971).

Table 1. Summary of character differences between *Zophobas atratus* and *Z. rugipes* after Spilman (unpublished data, pers. comm.).

Character	<i>Z. atratus</i>	<i>Z. rugipes</i>
Head width	broader	narrower
Elytral intervals	less convex	more convex
Elytral serial punctures	less impressed, not connected	more impressed, moderately connected
Antenna, basal angles of segments 9-11	sharp	rounded
Male protibia, curvature of apical half	entire tibia evenly curved	greater
Male mesofemur, granulation	smooth	numerous small granules
Male metafemur, postero-dorsal surface	concave	flat or convex
Paramere	narrower	broader

CROSSES. Between-population and within-population crosses were made among the beetles from 3 of the localities: Costa Rica, El Taladro and El Zamorano. The beetles were placed in sandwich boxes, 3 pairs to a box, at 28°C. At least 3 boxes of each cross were set up. Females laid their eggs through a screen into a layer of flour in the bottom of the box. The flour was sifted and the eggs counted once a week. The eggs were set aside to hatch, and the newly hatched larvae counted. This procedure was continued for 12 weeks until a substantial fraction of the adults had died.

MORPHOMETRY. The right antenna and right proleg of 10 beetles of each sex from all of the within- and between-population crosses were removed and mounted on cards in a uniform orientation. Their outlines were then drawn using a camera lucida. Basal angles of the penultimate antennal segments were measured from the drawings with a protractor. Using a digitizer and computer, the curvature of the protibia was estimated by drawing a base-line between the ends of the concave side of the tibia and dividing this line into 10 equal increments beginning at 5%, 15% . . . 95% of its length (Fig. 1). At each of these points, the distance (in mm) from the base-line to the concave margin of the tibia (y-coordinate) was determined, as was the real distance (mm) of each point from the apical end (x-coordinate) of the tibia. Total length of the tibia was also measured.

Shape was then estimated independently of tibial (hence, beetle) size by taking the ratio of the x and y coordinates. Because ratios are not normally distributed, and thus are not amenable to parametric statistics, the actual variable used was the log of the ratios [$\log(x/y)$] or the $\log x - \log y$ (Mosimann and James 1979). Under the lognormal assumption, differences in shape could then be tested using one-way Analysis of Variance (ANOVA) programmed on a Hewlett-Packard HP-11C Calculator.

RESULTS

CROSS-BREEDING. Because the number of females was not identical in all of the crosses and because beetles died throughout the experiment, the most satisfactory indices of breeding success were the number of eggs laid per female-week, larvae hatched per female-week and the proportion of the eggs hatched

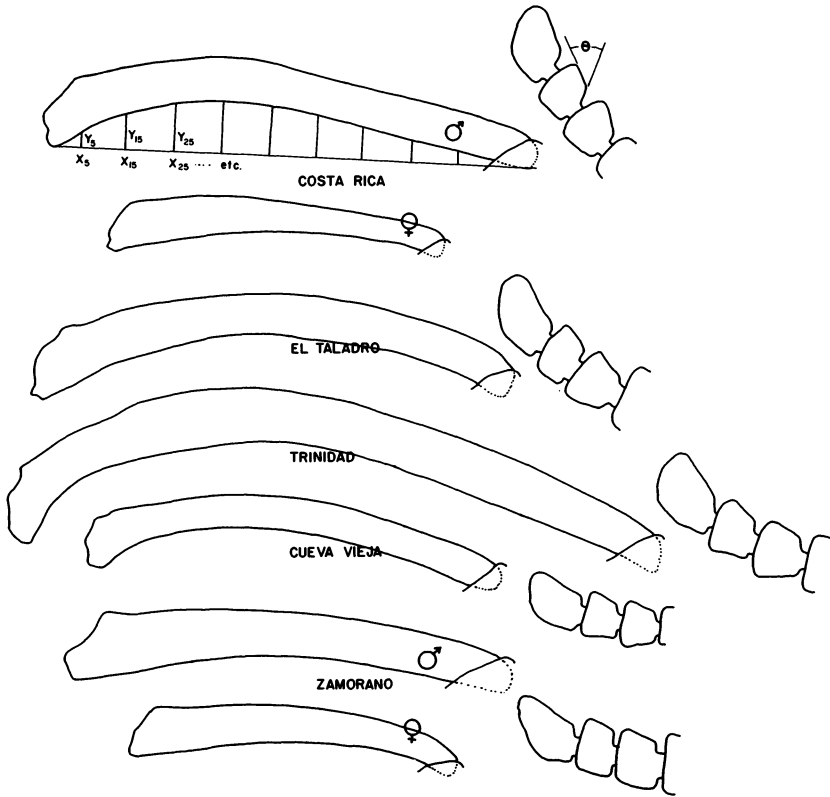


Fig. 1. Outline drawings of protibiae and terminal 3 antennal segments of representative males from populations studied. For comparison, a female protibia is shown for Costa Rica and El Zamorano populations. Sexual dimorphism of protibia is much less in *Z. atratus* (El Zamorano) than in *Z. rugipes* (all others). Method of estimating protibial shape and antennal angles is shown for Costa Rica example.

(transformed as $\arcsin\sqrt{\text{proportion}}$ to stabilize the variance for ANOVA). One-way Analysis of Variance indicated that beetle collection locality (cross) had no significant effect on the eggs per female-week, but did affect the larvae per female-week ($F = 7.79$; $P < 0.001$). Most of this seems to be the result of the effect of cross on the proportion hatched ($F = 13.88$; $P < 0.001$). Thus, all females are laying eggs at about the same rate, no matter what their source locality, but the fraction of the eggs which hatch and thus the larval production rate, depends strongly on the source locality of the males with which they are paired. For within-population crosses, 56–66% of the eggs hatched.

A Newman-Keuls test on the ranked means of larvae per female-week (Fig. 2A) shows that the within-population crosses had the highest larval production per female-week, but did not differ significantly from the two between-population hybrids with El Taladro females. There is broad overlap of rates with

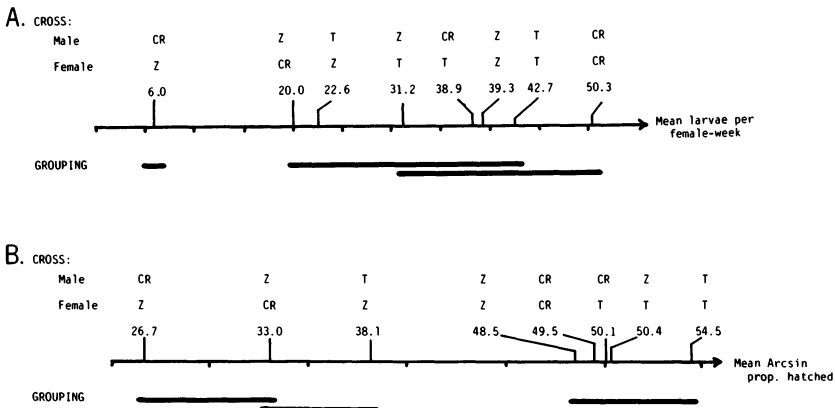


Fig. 2. Interbreeding success of the strains of *Zophobas*: Newman-Keuls tests for A) mean larvae per female week and B) mean arcsin $\sqrt{\text{proportion hatched}}$. Lines indicate means not significantly different at $P < 0.05$. CR = Costa Rica; Z = El Zamorano; T = El Taladro.

most of the hybrids, but the El Zamorano female \times Costa Rica male has a significantly lower rate than any other group.

Because larvae per female-week is the product of the eggs per female-week and the proportion hatched, each with its own variation, the success of interbreeding patterns can be clarified through a Newman-Keuls test on the ranked means of the arcsin $\sqrt{\text{proportion hatched}}$ (Fig. 2B). The within-population crosses and both between-population hybrids with El Taladro females are not significantly different from one another, but are higher than 3 of the crosses between beetles identified as *Z. rugipes* and *Z. atratus*. In this second group, differentiation is incomplete, but the El Zamorano female \times Costa Rica male is significantly lower than the El Zamorano female \times El Taladro male. The El Zamorano female \times Costa Rica male group has the lowest larvae per female-week as well as the lowest proportion hatched.

MORPHOMETRY. The different shapes of the male and female protibiae, as well as representative antennal tips, from the various localities are illustrated in Figure 1. When the mean $\log(x/y)$ (shape estimate) is plotted against the % of tibial length at which $(x/y)_i$ was determined, the tibial shapes can be compared across localities. When this is done for the males, it is apparent that most of the shape differences are found in the apical portion (5 to 40%) of the tibia (Fig. 3). A statistical comparison (ANOVA) of shape was made only for $\log x/y$ at 15% of tibial length [$\log(x/y)_{15}$] and showed that male tibial shape varies according to collection locality and hybrid ($F = 18.85$; $P < 0.001$). A Newman-Keuls test segregated these shapes clearly into 3 distinct groups, or 4 with some overlap between two of the groups (Fig. 4A). The shape of male El Zamorano tibiae was significantly less curved than all the others. All hybrids of El Zamorano with any other strain fell into a second group with significantly greater curvature than El Zamorano. All 5 members of these two groups were either *atratus* \times *atratus* or *atratus* \times *rugipes*. All those males identified as *rugipes*,

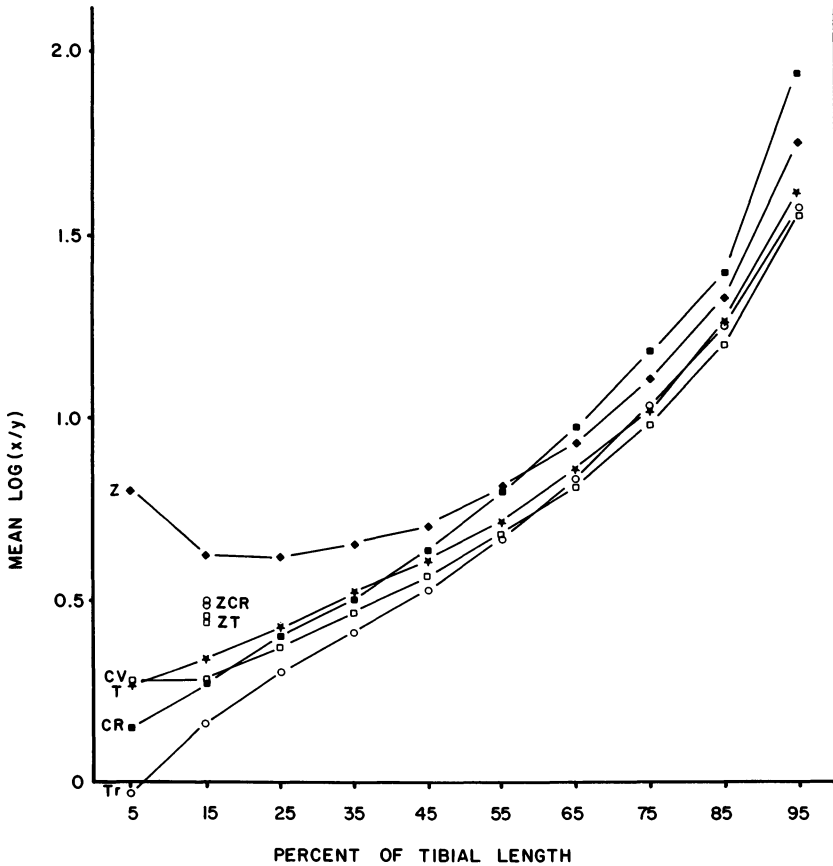


Fig. 3. Male protibial shape for 5 populations of *Zophobas*. Shape shown independently of size by plotting the log x/y against the % of tibial length (see text). Value of log x/y at 15% of tibial length shown for hybrids ($Z \times T$; $Z \times CR$) as well. The lower the left half of each curve, the more curved is apical half of tibia. See Figure 4 for abbreviations of localities.

or of hybrids between *rugipes* strains, clustered as 2 incompletely differentiated groups with still greater tibial curvature. Trinidad males showed the greatest curvature and were significantly different from El Taladro males, but not from other *rugipes* males or *rugipes* \times *rugipes* hybrid males.

Many organisms show a change of shape as size changes. Because both species are highly variable in size, allometry was tested for each group of male tibiae by plotting individual leg length against shape (log x/y) at 15% of length. A significant correlation would indicate that shape changes with size. Only the El Zamorano and Trinidad strains showed substantial allometry. The tibiae of Trinidad males became more curved as size increased, while those of El Za-

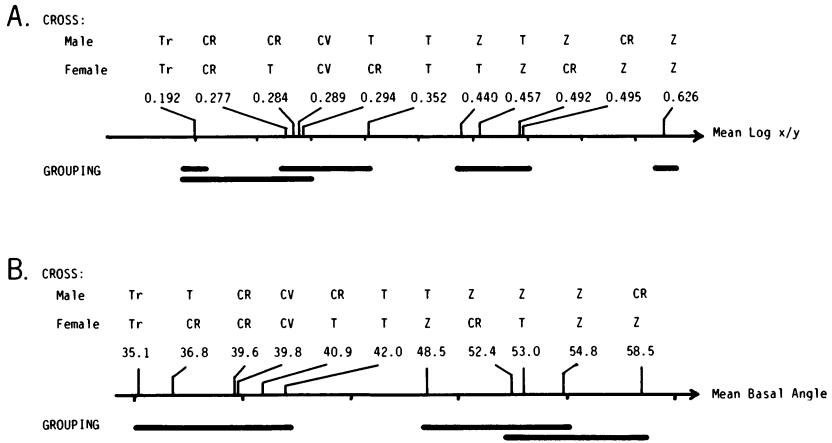


Fig. 4. Morphological variation among the strains and hybrids of *Zophobas*. Newman-Keuls tests for A) male protibial shape (mean $\log(x/y)$ at 15% of tibial length) and B) mean basal angle ($^\circ$) of penultimate antennal segment of males. Lines indicate means not significantly different at $P < 0.05$. Tr = Trinidad; CR = Costa Rica; T = El Taladro; CV = Cueva Vieja; Z = El Zamorano.

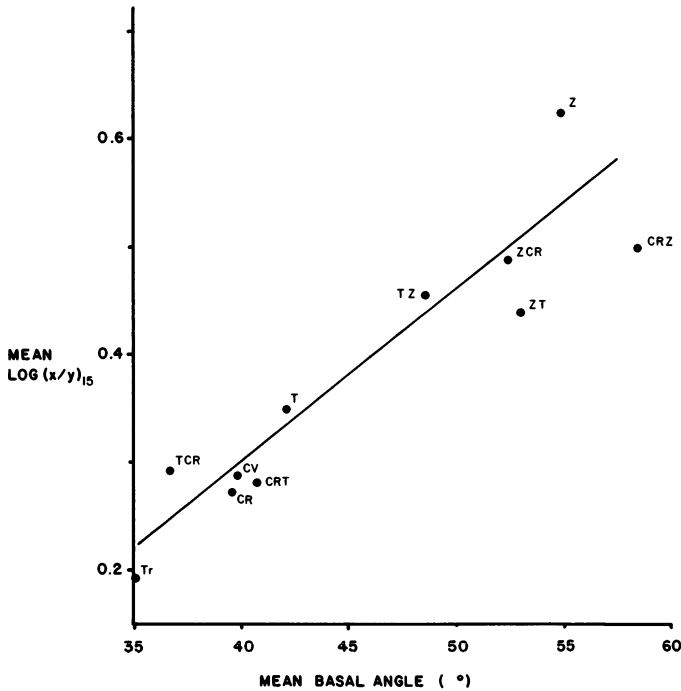


Fig. 5. Mean male protibial shape in relation to mean basal angle of penultimate antennal segment. Protibial shape estimated by $\log x/y$ at 15% of tibial length. Correlation between these two characters is high ($r = 0.919$). Crosses indicated by letters next to each point, male first. See Figure 4 for abbreviation of localities.

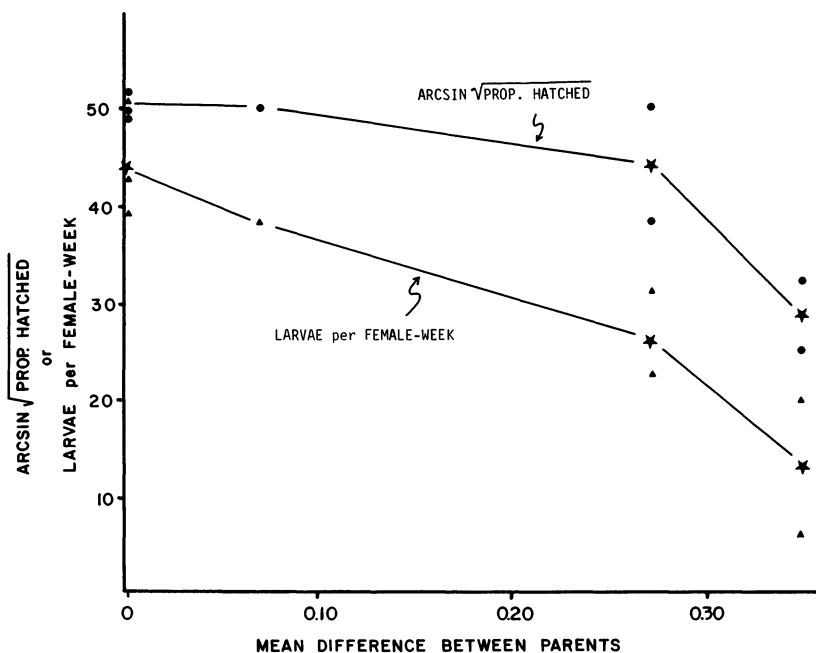


Fig. 6. Relationship between reproductive compatibility and degree of morphological difference between parents. Morphological difference estimated as difference in $\log(x/y)_{15}$, reproductive success as mean proportion of eggs hatched (arcsin $\sqrt{\text{proportion}}$ transformed), and mean larvae per female-week. Reproductive compatibility declines as morphological difference increases.

morano males became less curved. All other groups were variable, and showed only weak correlation, although most of the extremely small males had less curved protibiae. Overall, the relationships were sufficiently weak and the ranges of shape resulting from allometry sufficiently small that allometry was ignored in further analysis.

Analysis (ANOVA, Newman-Keuls test) of the basal angles of the penultimate antennal segments of males showed generally similar results. Those identified as *atratus* and their hybrids formed two broadly overlapping groups in which only the extreme means differed significantly (Fig. 4B). All *rugipes* and their crosses with other *rugipes* strains formed a second group with smaller antennal angles. The mean basal angle thus distinguishes quite clearly between *rugipes* and any beetles with *atratus* characters.

Not surprisingly, leg shape [$\log(x/y)_{15}$] is highly correlated with basal antennal angle ($r = 0.919$; Fig. 5). This is probably true as well for other characters (Table 1; not measured by me) distinguishing beetles identified as *Z. rugipes* and *Z. atratus*.

These measures allow estimation of the degree of morphological difference among the parent strains and to compare this with the success of interbreeding (Fig. 6). The degree of morphological difference between parents was estimated

by taking the difference of the mean $\log(x/y)$ for each pairing of parents and plotting this against both mean larvae per female-week and proportion hatched (transformed to $\arcsin\sqrt{\text{proportion}}$). As morphological difference between parents increases, irrespective of *rugipes* or *atratus* identity, the reproductive success of that cross decreases (Fig. 6). Morphological similarity thus correlates with breeding compatibility.

DISCUSSION

The data suggest that *Z. atratus* and *Z. rugipes* are morphologically distinct members of the same species. *Zophobas rugipes* Kirsch, 1866, is therefore synonymous with *Z. atratus* (Fab., 1775), the senior name. There is presently not enough information to decide whether the two morphological types are members of polytypic disjunct or conjunct populations, or whether morphological gradients (morphoclines) connect the *Z. atratus* type with the *Z. rugipes* type (Endler 1977). The data available to me indicate that the two types very rarely occur together (Spilman, pers. comm.). Whatever the situation, some factor maintains sufficient genetic difference among these populations to keep them morphologically distinct and reproductively of lower compatibility. Endler (1977) discusses how such differentiation might be caused and maintained, but it seems premature to speculate on these matters here. It seems likely that at least large populations of both types are disjunct because of the disjunct nature of bat guano or other deposits of organic debris in which the beetles live. Low population density between such large populations would be a partial barrier to gene flow, especially if the species were not very vagile, but whether this bears on the present problem is unknown. It is also not known whether there are subtle habitat preference differences between these two morphological types.

It is interesting to view the geographic pattern of reproductive compatibility of the three interbred strains. The localities in Honduras are separated by less than 100 km, while the Costa Rican locality is about 600 km from either of these. Compatibility of the *Z. atratus* (El Zamorano) with the closer *Z. rugipes* (El Taladro) was higher than with the more distant *Z. rugipes* (Costa Rica). Compatibility of *Z. rugipes* (Costa Rica \times El Taladro) from the distant localities was not significantly different from the within-population crosses.

Finally, many species of *Zophobas* are difficult to distinguish (Spilman, pers. comm.). The methods I have applied here may be generally applicable to this problem genus.

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LITERATURE CITED

- ENDLER, J. A. 1977. Geographic variation, speciation and clines. Monographs in Population Biology, No. 10. Princeton Univ. Press.
 MOSIMANN, J. E., AND F. C. JAMES. 1979. New statistical methods for allometry with application to Florida red-winged blackbirds. *Evol.* 33:444-459.

- Tschinkel, W. R. 1978. Dispersal behavior of the larval tenebrionid beetle, *Zophobas rugipes*. *Physiol. Zool.* 51:300-313.
- . 1981. Larval dispersal and cannibalism in a natural population of *Zophobas atratus* (Coleoptera: Tenebrionidae). *Anim. Behav.* 29:990-996.
- , AND G. VAN BELLE. 1976. Dispersal of larvae of the tenebrionid beetle *Zophobas rugipes*, in relation to weight and crowding. *Ecol.* 57:161-168.
- , AND C. D. WILLSON. 1971. Inhibition of pupation due to crowding in some tenebrionid beetles. *J. Exp. Zool.* 176:137-146.

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LITERATURE NOTICES

- Yandell, K. L. 1984. Sound production of *Dendroctonus ponderosae* Hopkins (Coleoptera, Scolytidae): a comparison of populations from three host pines in Oregon. *Z. ang. Ent.* 97:180-187.
- Emetz, V. M. 1984. Dynamics of phenotypical composition and level of asymmetry of the number of fossae on elytra of imago in a population of *Pterostichus oblongopunctatus* (Coleoptera, Carabidae) on recreation territory. *Zool. Zhurn.* 63:218-221 (in Russian).
- Mikheev, A. V., et al. 1984. Relations host plants and structure of a willow race of *Lochmaea capreae* (Coleoptera, Chrysomelidae). *Zool. Zhurn.* 63:209-217 (in Russian).
- Maddison, W. P., M. J. Donoghue, and D. R. Maddison. 1984. Outgroup analysis and parsimony. *Syst. Zool.* 33:83-103.
- Mann, J. S., and R. A. Crowson. 1984. On the digitiform sensilla of adult leaf beetles (Coleoptera: Chrysomelidae). *Entom. Gener.* 9:121-133.
- Olexa, A. 1984. Revision der Arten der Gattung *Pholioxenus* Reichardt (Coleoptera, Histeridae). *Acta ent. bohemoslov.* 81:113-131.
- Vaněk, S. 1984. Larvae of the palaeartic species *Clivina collaris* and *Clivina fossor* (Coleoptera, Carabidae, Scaritini). *Acta ent. bohemoslov.* 81:99-112.
- Löbl, I. 1984. Les Scaphidiidae (Coleoptera) du nord-est l'Inde et du Bhoutan I. *Revue suisse Zool.* 91:57-107.
- Pace, R. 1984. Aleocharinae delle Mascarene, parte I: tribu Myllaenini, Pronomaeini, Oligotini e Bolitocharini (Coleoptera, Staphylinidae) (XLV Contributo alla conoscenza della Aleocharinae). *Revue suisse Zool.* 91:3-36.
- Wood, S. L. 1984. New synonymy and new species of American bark beetles (Coleoptera: Scolytidae), part X. *Great Basin Natural.* 44:113-119.
- Forge, P. 1981. Coléoptères. Chapter 21, pp. 487-516. In: Durand, J.-R. et C. Lévêque (editors). *Flore et faune aquatiques de l'Afrique sahélo-soudanienne*. O.R.S.T.O.M., Paris. 2 vols., 873 pp.
- Costa, C. 1983. Revisão do gênero *Deilelater* Costa, 1975 (Elateridae, Pyrophorinae), com a descrição de nova espécie. *Revta. bras. Ent.* 27:115-124.
- Martins, U. R. 1983. Sinonímias, nova combinação e novas espécies em *Aerenicopsis* Bates (Aerenicini) e *Trichohippopsis* Breuning (Agapanthini) (Coleoptera, Cerambycidae, Lamiinae). *Revta. bras. Ent.* 27:161-163.
- Almeida, L. M. de, and R. C. Marinoni. 1983. Contribuição ao conhecimento de gênero *Psyllobora* Chevrolat, 1837 (Coleoptera, Coccinellidae). *Revta. bras. Ent.* 27:165-175.
- Holeski, P. M. 1984. Possible colonization strategies of some carabid beetles inhabiting stream shores (Coleoptera: Carabidae). *Great Lakes Ent.* 17:1-7.
- Galewski, K. 1982. Descriptions of the first and third stage larvae of *Agabus striolatus* (Gyll.) (Coleoptera, Dytiscidae). *Bull. Ac. Pol. Biol.* 30:75-80.