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RELATIVE ABUNDANCE, PHENOLOGY AND FLOWER VISITS OF APID BEES IN EASTERN PARANÁ, SOUTHERN BRAZIL (HYMENOPTERA, APIDAE)¹⁾²⁾

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While extranidal activities of apid bees have been relatively well studied in temperate regions, our knowledge on this problem is still incomplete in tropical and subtropical regions. The present paper deals with relative abundance, phenology and flower visits of apid bees under subtropical climate, studied at two grassland areas in and near Curitiba, the State Capital of Paraná. The work was originally undertaken for periodic sampling of all wild bees throughout the year. From the data obtained, the part dealing with Apidae, all specimens of which were identified to species, was extracted and used for the present paper.

1) A joint contribution from the Zoological Institute, Faculty of Science, Hokkaido University, Sapporo, Japan, 060 (SFS, No. 915) and Departamento de Zoologia, Faculdade de Filosofia, Ciências e Letras, Universidade Federal do Paraná, Curitiba, Paraná, Brasil (SL, No. 301).

2) Wild bee biofaunistics and biocoenotics in Eastern Paraná, South Brazil. III.

Methods and areas surveyed

The surveys were made from March, 1962 to February, 1963 at São José dos Pinhais near Curitiba, and from August, 1963 to September, 1964 at Boa Vista in Curitiba. The two localities are henceforth abbreviated as SJP and BV respectively. In both areas samples were taken regularly, three times per month, with four (SJP) or three (BV) hours of collecting per sample. During each sampling hour all wild bees found on flowers or in flight were captured as far as possible, irrespective of their relative abundance, and separately preserved according to the flower species visited. In subsequent descriptions, each regular sampling is abbreviated as I-1 (early January), IV-2 (mid April), X-3 (late October), etc. Further details of the procedures are given in a previous paper (Sakagami, Laroca and Moure 1967a).

The survey at SJP was made at a secondary grassland near Airport Afonso Pena, the environmental conditions of which were given in the paper cited. Sampling was limited to one hour for VI-1 and VII-3 and two hours for VII-1 due to cold weather and to two hours for X-3 due to rain. The survey at BV was made within an area approximately 2×2 km sq., covering three different habitats, edaphic grassland, caprice with shrubs of 0.5–3 m high and ruined gallery forest. Therefore the area was vegetationally more complicated than at SJP. Periodic sampling was far less complete than at SJP for various causes as follows: IV-3, V-3, VI-3, VIII-1, VIII-2, not surveyed; IX-3, XII-2, XII-3, IV-2, adverse weather, later rained; V-1, strong wind; VII-1, VII-2, cold weather. Moreover, the number of bees captured was generally small from April to August, except for VII-3 and VIII-3.

Species collected and their relative abundance

The species collected in both surveys are listed below, the specimens captured in each 10 day period given separately, together with flowers visited. Symbols "p" and "w" mean respectively female with pollen loads and worker. The generic system used for stingless bees follows that by Moure (1951, 1961).

1. *Eulaema* (*Apeulaema*) *nigrita* Lepeletier 1841. BV (1♀):X-1.
2. *Bombus* (*Fervidobombus*) *morio* (Swedrius 1787). SJP (1w):II-2, *Vernonia* sp. BV (1w 1♂):II-1, 1w; III-1, 1♂, *Vernonia westiniana*. This species prefers warmer areas with more trees, being relatively rare in and near Curitiba.
3. *Bombus* (*Fervidobombus*) *bellicosus* Smith 1879. SJP (25♀♀ 5♀♀ or ww 236 ww 62♂♂, cf. Fig. 2. Among these specimens 2 ww and 4♂♂ were not examined as to relative age and do not appear in Fig. 2). BV (1♀ 1w 1♂):IX-2, 1♀, *Senecio mattfeldianus*; I-3, 1♂; II-3, 1w. This species is typically an inhabitant of Pampas with the center of distribution in and near Buenos Aires. It reaches the highlands of Paraná where relatively isolated populations, including that in SJP, are recorded from several localities. As described by Moure and Sakagami (1962), females are relatively constant in color pattern while males quite variable.
4. *Bombus* (*Fervidobombus*) *atratus* Franklin 1913. SJP (15♀♀ 44ww 7♂♂, cf. Fig. 2, 1w not shown as in *B. bellicosus*); BV (10♀♀ 39ww 3♂♂, cf. Fig. 2, 1w not shown). This is the commonest lowland bumblebee in southern South America, though outnumbered by *B. bellicosus* at SJP. As already mentioned (Moure and Sakagami 1962) the species is polytypic with the color varying from completely black to distinctly yellow banded. Most specimens from SJP and BV belong to the flavinic type, which prevails in the highlands of the States of Paraná and Santa Catarina.
5. *Trigona* (*Trigona*) *spinipes* (Fabricius 1793). SJP (675ww); BV (151ww) (cf. Table 1). One of the commonest stingless bees in southern Brazil.
6. *Plebeia* (*Plebeia*) *emerina* (Friese 1900). SJP (1w):XII-1, *Xyris* sp. BV (3ww):I-1, 2pp, *Jusseiaea sericea*: III-3, 1p. One of the commonest stingless bees at woodlands near and in Curitiba, even in the center of the city.
7. *Plebeia* (*Schwarziana*) *quadripunctata* (Lepeletier 1936). BV (10ww): I-1, 1w, *Elephantopus mollis*; II-1, 3pp, *Vernonia westiniana*; II-3, 1p, *V. westiniana*; IV-1, 1p, *V. westiniana*, 1p. *Eupatorium* sp. 1; IV-2, 2pp, *Eup.* sp. 1, 1w, *Baccharis* sp. 5.
8. *Nannotrigona* (*Scaptotrigona*) *bipunctata* (Lepeletier 1836). BV (24ww): VIII-3, 1p. *Senecio oleosus*; IX-1, 1p. *S. oleosus*; X-2, 1p; I-2, 2ww, *Baccharis* sp. 2; III-1, 3pp, *Eryngium eburneum*;

III-2, 4pp, *E. eburneum*; IV-1, 1w *Eupatorium* sp. 1, 5pp 3ww, *E. eburneum*; IV-2, 2pp, *E. eburneum*; V-1, 1p. *E. eburneum*.

9. *Melipona nigra schrencki* Gribodo 1893. BV (3ww):II-1, 3ww, *Vernonia westiniana*.

10. *Melipona quadrifasciata quadrifasciata* Lepeletier 1836. SJP (9ww 2♂♂): V-1, 1♂ *Cunila gallioides*; V-3, 1w, *Baccharis erioclada*; VI-2, 1w, *Senecio* sp. 1; VI-3, 4ww, *S.* sp. 1; IX-2, 1w, *Croton* sp.; XII-1, 2ww 1♂, *Eupatorium* sp. 7. BV (1♀ 63ww 1♂):VIII-3, 1p, *Senecio oleosus*; IX-1, 1w, *S. oleosus*; XI-3, 1p, *S. brasiliensis*, 1w, collecting resin from *Araucaria angustifolia*; XII-3, 1♀, caught by an asilid fly *Malophora* sp., certainly during nuptial flight; I-3, 6pp 26ww 1♂, *Vernonia westiniana*; II-1, 4pp 13ww, *V. westiniana*; II-2, 2pp 4ww, *V. westiniana*; III-1, 1p, *Solanum* sp. 1; III-3, 2ww, *V. westiniana*.

(11.) *Apis mellifera* Linné 1758. The European honeybee workers were not captured but quantitatively outnumbered all wild bees in most months (Table 1). Most individuals had pale coloration, showing a genetic predominance of the Italian race, *A. m. ligustica* Spinola. In order to have an estimate for relative abundance, both honeybees and wild bees were sampled without choice on March 5, 1962 for two hours. The species and individuals collected are in descending order as follows: *Apis mellifera* 74 ww, *Bombus bellicosus* 10ww, *B. atratus* 7ww 1♂, *Trigona spinipes* 8ww, *Augochloropsis iris* 6♀♀ 1♂, *A. sp.* 1 4♀♀, *Hylaeus rivalis*, *Melissoptila pterocauli*, *Gaesischia fulgrans* each 2♀♀, *Colletes rugicollis*, *Megachile lentifera*, *Exomalopsis* sp. 1 each 1♀. Therefore the honeybees constituted ca. 61.6 % of the total bees sampled. At SJP a nest of honeybees was found on January 21, 1963 in an abandoned termite nest about 40 cm high.

The relative abundance of various species at the two areas is compared in Fig. 1 by using the occurrence probability method of Kato (cf. Sakagami and Matsumura 1967).

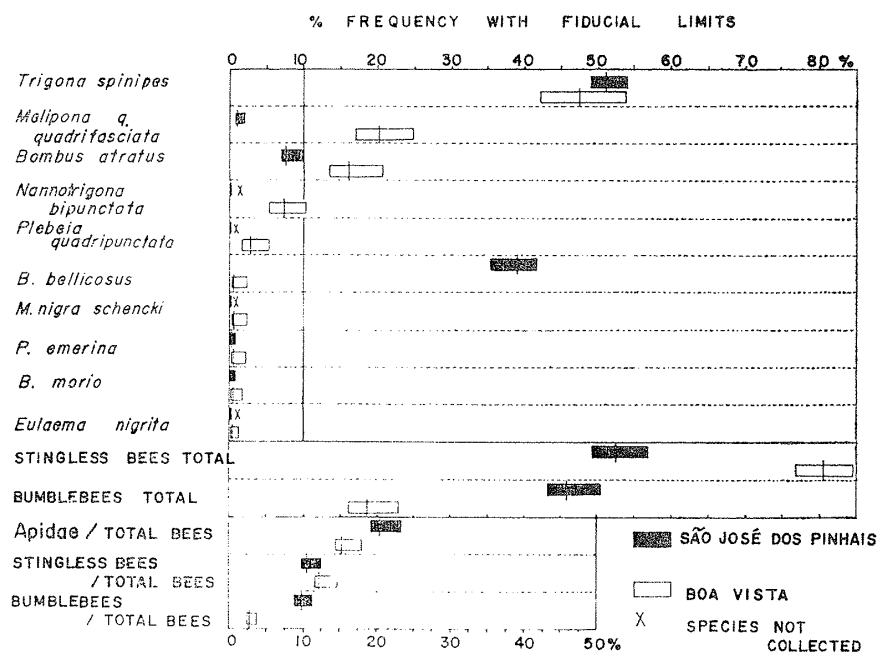


Fig. 1. Relative abundance of apid species at São José dos Pinhais and Boa Vista, shown by occurrence probability method.

The species are arranged from the top in descending order of individual number sampled at BV. The percentage ratio of each species is given by horizontal bars, the ends of which show the upper and lower fiducial limits ($p=0.05$) and short vertical lines, the percentage ratios. Similarly the percentage ratios of total stingless bees and total bumblebees are given below. Three bottom graphi show the percentage ratios of total Apidae, total stingless bees and total bumblebees to total wild bee individuals sampled. On XI-1, SJP, an abnormally high number of workers of *Trigona spinipes*, 281, was recorded. A calibration

was made by substituting this figure by 43 (=average number of individuals of this species sampled on VIII-3, 35, and IX-2, 51) and this figure was used to prepare Fig. 1.

The vertical line in the figure shows the reciprocal of the combined number of species collected at both areas. Regarding the species exceeding this line as dominants, *Tr. spinipes* and *B. bellicosus* at SJP, and *Tr. spinipes*, *M. quadrifasciata* and *B. atratus* at BV are considered as dominant. Comparing the two areas, *B. bellicosus* is significantly more abundant at SJP while *M. quadrifasciata* and *B. atratus* are more abundant at BV. Although not dominants, *N. bipunctata* and *P. quadripunctata*, collected only at BV, also show a significant difference. At the generic level, stingless bees are significantly more abundant at BV and bumblebees, *vice versa*. The percentage ratio of Apidae to total wild bees is significantly higher at SJP (845 out of 3,979 individuals in calibrated figures) than at BV (315/1,920), mainly because of the abundance of bumblebees at SJP.

The causes of these differences are not clear but probably in part depend on the differences in habitat. The vegetation of BV is richer in trees and nearer to woodland habitat than at SJP. These conditions must be favorable for stingless bees, most of which have an intimate connection with arboreal vegetation. This assumption is also supported by the faunal makeup. Concerning bumblebees, three out of four species inhabiting Eastern Paraná are represented at both areas, only one species, *B. (Fervidobombus) brasiliensis* Lepeletier, which in Paraná is confined to the western slope of the Serra do Mar, being absent. On the other hand, some stingless bee species known from woodland habitats in and near Curitiba, such as *Melipona marginata* Lepeletier, *Paratrigona lineata* (Lepeletier), *Plebeia droryana* (Friese), *Nannotrigona testaceicornis* (Lepeletier), *Partamona cupira* (Smith), *Plebeia remota* (Holmberg) and *Trigona (Tetragonisca) jaty* Smith, are not included in either locality. Further, *Plebeia emerina*, one of the commonest species in and near Curitiba, is represented by few individuals. The predominance of *T. spinipes* is easily understood because of its construction of aerial nests and independence from tree hollows. Further comparison of the relative abundance of stingless bees between woodland and grassland areas would be interesting when analysed in connection with the difference in modes of life among various species.

Phenology

A single female of *Eulaema nigrita* captured in mid spring carried sand particles on her hind legs, indicating her participation in nest construction, though the use of sand is so far unknown in Euglossinae (*cf.* Zucchi, Sakagami and Camargo 1969). Except for this parasocial species, the other eusocial forms captured are bionomically divided into two groups, bumblebees and stingless bees (with honeybees), corresponding to primitively and highly social bees in the terminology by Michener (1969). This distinction is also valid for their response to the seasonal change of climate so that they are separately dealt with.

1. *Phenology of bumblebees:* The bionomics of the South American bumblebees is of particular interest from the standpoint of comparative bee sociology. Being a typical Holarctic group, the bumblebees seldom reach the Palaeotropical lowlands.¹⁾ On the other hand, due to the latitudinal continuity of gigantic mountain ridges in New World, they are distributed in South America southwards nearly to the Magellan Strait, with six species endemic to tropical and subtropical lowlands (Moure and Sakagami 1962). The bionomic differences between these lowland species and their north temperate cousins were once claimed by v. Ihering (1903). His opinions assuming the perennial colony life with pleometrotic association and establishment of new colonies by means of swarming have

1) One species, *B. abditus* Tkalců, was recently recorded as a relic from equatorial Africa (Tkalců 1966).

been cited for nearly half a century without critical studies. Only recently some papers dealing with these tropical species have been published (Dias 1958, Moure and Sakagami 1962, Sakagami and Zucchi 1965, Sakagami, Laroca and Moure 1967b). Among various problems concerning their mode of life, the phenology or annual cycle is here considered on the basis of our periodic sampling data.

The presence of perennial colonies was confirmed for *B. atratus* by Kerr in Rio Claro, the State of São Paulo (*cf.* Sakagami and Moure 1962), and, though under artificial condition, by Zucchi (unpublished). But this does not necessarily mean that all colonies can survive more than one year or that the colony life is semiindependent from the seasonal weather changes as in highly social bees. Even in the humid tropical climate of the Amazonic basin, *B. transversalis* (Olivier) shows certain seasonal trends in the appearance of the three castes. Such a seasonal trend is clearly seen in our results presented in Fig. 2. In both *B. atratus* and *B. bellicosus*, queens are mainly collected from August to November and sporadically from late March to May. The former individuals indicate the activities of colony founding and foraging before the appearance of workers. In early October queens were observed at both areas flying in search of nesting sites. On the other hand, queens collected from March to May apparently represent the newly emerged individuals, as suggested by their relatively fresh wings. Their scarcity corresponds to the experience familiar in northern Hemisphere, where new queens in fall are collected less abundantly than in spring.

The appearance of males phenologically coincides well with these new queens, and worker activities are most intense in the months between the two periods of activities of queens. Consequently the pattern of the annual cycle basically does not differ from

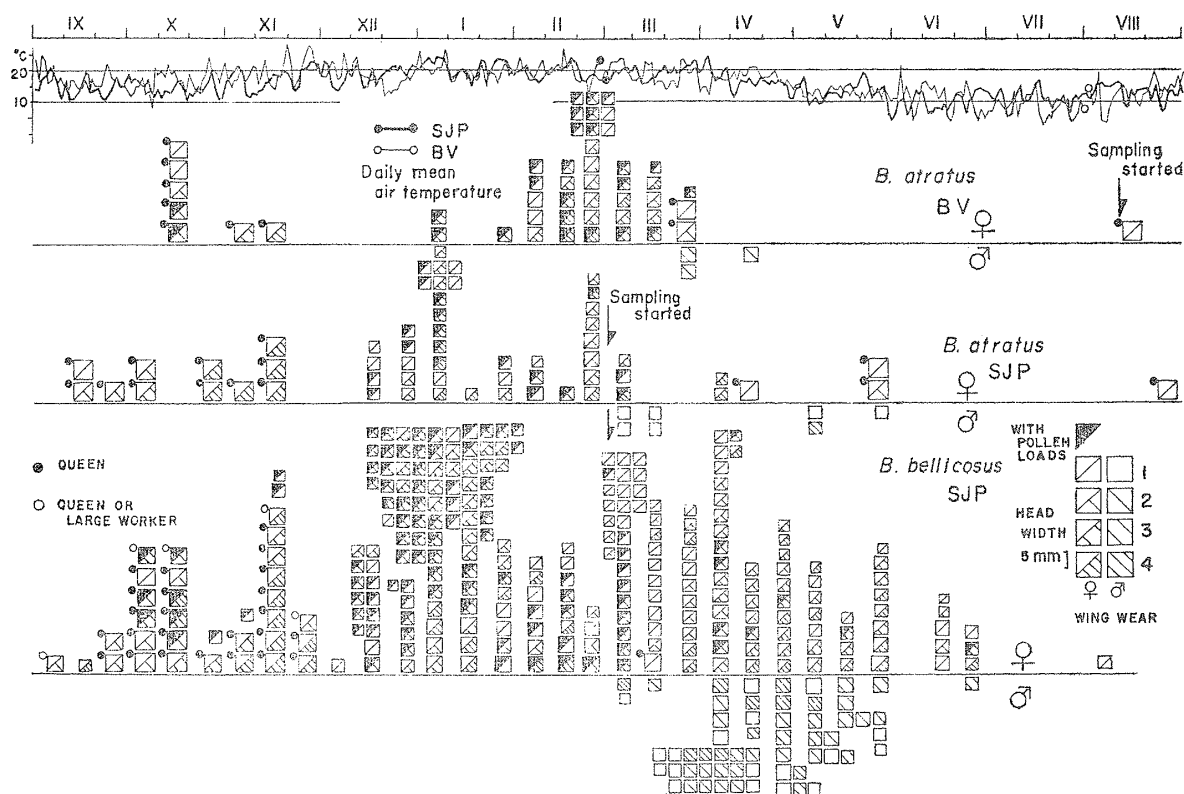


Fig. 2. Phenology of bumblebees at São José dos Pinhais (SJP) and Boa Vista, Curitiba (BV), each based upon one year's periodical sampling. Each individual is shown by a square, the size of which corresponds to body size (=head width), with indication of relative age estimated by wing wear, each on a scale of 1~4. Females with pollen loads are shown with black triangles.

Table 1. Seasonal change in the abundance of *Trigona spinipes* (capture

Sao José dos Pinhais							
Trigona							
Month		N	P	R	T	TT	Apis
Sep	1	48	6	227	281	501	>
	2	5	1	45	51	181	>
	3	6	4	5	15	89	>
Oct	1	1	1		1	22	>
	2					52	>
	3		2		2	56	>
Nov	1	5	16	35	56	121	>
	2	1	2		3	78	>
	3	1			1	79	>
Dec	1	1	6	3	10	262	>
	2	11	36	6	53	522	>
	3	3		2	5	107	>
Jan	1					141	<B
	2	1			1	64	<B
	3	3	5		8	152	>
Feb	1	2	4		6	89	>
	2	2	6		8	66	>
	3	5			5	86	>
Mar	1	2			2	100	>
	2	15	1	6	22	68	±
	3		2		2	50	±
Apr	1					52	>
	2	1	2		3	56	+
	3	1			1	91	?
May	1					190	?
	2	2	3		5	62	>
	3	1	8		9	55	>
Jun	1					0	±
	2	8	8	4	20	50	>
	3	8	7	7	22	186	>
Jul	1					0	±
	2					0	±
	3	2		3	5	130	>
Aug	1	3		14	17	205	>
	2	1	17	8	26	128	>
	3	8	1	26	35	128	>

P, with pollen loads; R, with resinous loads; N, without loads; T, total; TT, total wild
 <B, *Apis* less abundant than

that in north temperate species. However, a difference is found in the marked prolongation of the active period. In north temperate species the active period seldom exceeds eight months, from March to October, often much shorter in northern areas, or in *Pyrobombus*, many species of which are characterized by a short annual cycle. In Eastern Paraná, adult bees are collected virtually in any month except July. Moreover some workers collected in May and June carried pollen loads on their hind legs, suggesting brood rearing into late fall or even early winter. Two workers of *B. bellicosus* captured in mid August and mid September suggest that some colonies can survive during winter. A similar condition is

records) and *Apis mellifera* (relative estimates) at SJP and BV.

Boa Vista						Resin collecting by <i>Apis</i> (a) and <i>Trigona</i> (t) on:
<i>Trigona</i>						
N	P	R	T	TT	<i>Apis</i>	
2	2	3	3	86	>	<i>Senecio oleosus</i> (t) " (")
		8	9	127	+	
		1	5	40	>	
10		13	23	111	>	<i>Araucaria angustifolia</i> (t, a)
2	7		9	65	+	" (" , ")
	7		7	110	>	" (" , ")
3	5	3	11	78	>	" (t)
12		2	14	71	>	" (t, a)
6		1	7	64	>	
6	2	1	8	58	>	" (t, a)
				0	0	
				21	<	" (a)
				36	<	
3	1	6	7	61	>	<i>Baccharis</i> (t)
		15	18	90	>	" (")
		6	9	106	>	" (")
1			1	77	>	" (")
2	6	2	10	126	>	
				58	+	
				36	>	
1			1	11	+	
				46	>	
				32	>	
.....						
	1		1	18	0	
				8	0	
.....						
1	1		2	27	0	
					>	
.....						
	2		2	3	>	
				1	±	
				179	>	
.....						
.....						
1		2	3	174	<	<i>Senecio oleosus</i> (t)

bees; > and <, *Apis* more abundant or less abundant than all wild bees combined;
Bombus bellicosus.

seen in *B. terrestris* Linné introduced from England to New Zealand. In the South Island, N.Z., sometimes nests survive to the next spring (Gurr 1961) and this seems more frequent in the North Island (Cumber 1954). Probably such deviation from the typical annual cycle of north temperate species increases in northern areas of the South American lowlands.

2. *Phenology of stingless bees and honeybees*: In contrast to bumblebees, both stingless bees and honeybees are relatively independent from the seasonal change of weather trends. Their reproductive activity may have some correlation with seasons, but foraging activity continues throughout the year under subtropical conditions, only being inhibited

by adverse weather. Table 1 presents the seasonal change of the abundance of *Trigona spinipes* and *Apis mellifera*, shown respectively by capture records and relative estimates. The seasonal change of *T. spinipes* is characterized by its irregularity independent of seasons. The weather conditions at sampling may be partly responsible for erratic changes but cannot explain them completely, as shown by the frequent discrepancy between the number of individuals captured of *T. spinipes* and of total wild bees. It is assumed that the areas surveyed, especially of SJP, formed only a part of the foraging range of colonies of this species, which visited there only when favorable food and resin sources were present, or possibly the presence of such sources were communicated by scout bees. The same interpretation applies to *M. q. quadrifasciata* and *N. bipunctata* at BV, most individuals of which were collected in relatively limited periods, respectively late January – mid February and March – April. To verify this assumption, however, we need closer studies on the flight ranges of various stingless bees.

The honeybees outnumbered wild bee species virtually throughout the year. They were found on flowers in mid winter, even when no wild bees were collected. Further, they were found in early morning and late afternoon when wild bees were still or already not seen on flowers. How the numerical predominance of this introduced species with an outstanding foraging efficiency affects the activities of wild bee species would be an interesting problem but, for the time being, difficult to analyse quantitatively.

Table 2 shows the seasonal change in the percentage ratio of the individuals of apid bees to total wild bees captured at SJP and BV. The percentage ratio is, as already described, in general higher in SJP than in BV. At both areas the ratio is relatively low in winter but generally characterized by irregular fluctuation, explained in part by the behavior of the foraging populations of stingless bees as suggested above.

Table 2. Seasonal change in total number of apid bees/total number of wild bees (percentages of apid bees in parentheses).

Month	São José dos Pinhais		Boa Vista	
September	355/771	(46.1)	19/253	(7.5)
October	21/130	(16.2)	46/286	(16.1)
November	80/278	(29.7)	36/213	(16.8)
December	104/891	(11.7)	9/79	(11.4)
January	107/357	(30.0)	68/187	(36.3)
February	42/241	(17.5)	78/309	(25.2)
March	83/218	(38.1)	28/105	(26.7)
April	82/199	(42.1)	20/78	(25.6)
May	58/307	(18.9)	2/26	(7.7)
June	56/236	(23.7)	2/27	(7.4)
July	5/130	(3.8)	2/183	(1.1)
August	80/461	(17.3)	5/174	(2.9)
Mean percentage	25.6		16.4	

Flower visits

Both at SJP and BV most individuals were captured on flowers. Using the flower record of each specimen, some tendencies in relative flower visits are described below. Fig. 3 presents the percentage flower visits in several bee assemblages to some plant groups at SJP, by using the occurrence probability method as in Fig. 1. The assemblages compared are as follows: T♀ (Total female wild bees taken, 2,944 individuals), T_P (*Ditto*, females with pollen loads, 1,447), T♂ (*Ditto*, males, 978), A♀ (Total apid bees, females=queens+workers, 742), A_P (*Ditto*, those with pollen loads, 256), A♂ (*Ditto*, males, 70, mostly ♂♂ of *B. bellicosus*), S♀ and Sp (Total stingless bee females, 432, and those with pollen loads, 135, both mostly *Tr. spinipes*), B♀ and B_P (Total bumblebee females, 310, and

those with pollen loads, 121), *B. bellicosus* females (242) and the same species with pollen loads (101). In T, A and S, the figures are calibrated with respect to *Tr. spinipes* as noted previously.

The percentage of visits was first compared between Compositae and non Compositae, considering the overwhelming importance of the former group. Further the percentage ratio of visits with upper and lower fiducial limits ($p=0.05$) were calculated and illustrated in Fig. 3 for the following plant groups: I. Compositae, *Senecio* (4 spp., predominants, *E. sp. 7*, *E. litorale* and *E. sp. 2*), *Baccharis* (9 spp., predominants, *B. spicata*, *B. cylindrica*, *B. recurva*, *B. axillaris*), other genera (*Vernonia* 4 spp., *Calea* 2 spp., *Erigeron* 2 spp., *Achyrocline*, *Solidago* and an undetermined genus each 1 sp., predominants, *V. sp. 2*, *Calea hispida*). II. Non Compositae, Euphorbiaceae (1 sp., *Croton sp.*), predominants, *V. sp. 2*, *Calea hispida*). II. Non Compositae, Euphorbiaceae (1 sp., *Croton sp.*), predominants, *V. sp. 2*, *Calea hispida*). Saxifragaceae (1 sp., *Escallonia montevidensis*), Labiatae (3 spp., mostly *Cunila gallioides* and *Salvia lachnostachys*), Rosaceae (2 spp., nearly all *Prunus sp. 1*), Xyridaceae (1 sp., *Xyris sp.*), Boraginaceae (1 sp., *Moritzia dusenii*), other 13 families (24 spp.).

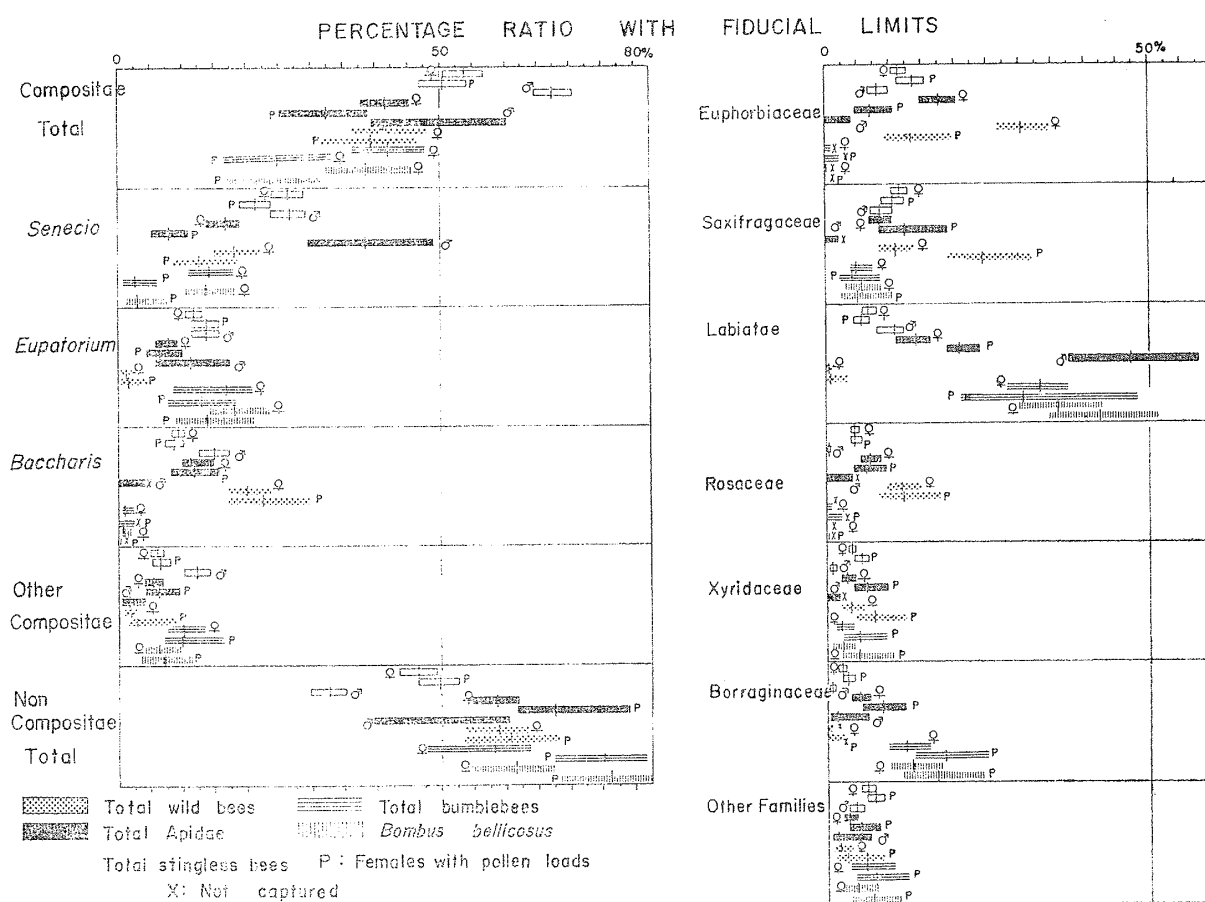


Fig. 3. Comparison of flower visits by all wild bees in relation to some selected assemblages of apid bees at SJP, shown by occurrence probability method.

Some results obtained from Fig. 3 are summarized below. Each bee assemblage is arranged in descending order of the percentage visits with " \geq ", and the symbol ">" indicates a significant difference shown by the nonoverlap of horizontal bars in the figure.

1) Percentage visit to Compositae is in ♀♀ $T > B \geq A \geq S$ and in pp $T > S \geq A \geq B$. Further, non Compositae > Compositae is seen in ♀♀ and pp of A, B and S. Therefore, the relative visit to non Compositae is significantly higher in Apidae than in total wild bees.

2) Within Compositae, the following tendencies are observed: *Senecio*, ♀♀ $T > S \geq A \geq B$; pp $T > S \geq A \geq B$ and $S > B$; ♂♂ $A > T$. *Eupatorium*, ♀♀ $T \geq B > A \geq S$; pp $T \geq B > A \geq S$. *Baccharis*, ♀♀, pp $S > T \geq A > B$, ♂♂ $T > a$ (small letters=absence of visits). Other genera, ♀♀, pp $B > T \geq A \geq S$; ♂♂ $T > a$. Consequently the low relative visits of Apidae to Com-

positae are mainly caused by those to *Senecio* and *Eupatorium*. Moreover, the relative visits to *Eupatorium* and *Baccharis* are reversed between stingless bees and bumblebees.

3) Among non Compositae the tendencies observed are: Euphorbiaceae, ♀♀ $S > A > T > b$, pp $T > S > A > b$, ♂♂ $T > a$; Saxifragaceae, ♀♀, pp $S \geq T \geq A > B$, ♂♂ $T > a$; Labiatae, ♀♀ $B > A > T > S$, pp $B \geq A > T > S$, ♂♂ $A > T$; Rosaceae, ♀♀ $S > A > T > B$, pp $S > A > T > B$ and $S > T$, ♂♂ $T > a$; Xyridaceae, ♀♀ $T \geq A \geq S \geq B$ and $T > B$, $S \geq T \geq A \geq B$, ♂♂ $T > a$; Borraginaceae, ♀♀ $B > A > T > s$, pp $B > A > T > s$, ♂♂ $T > A$; other families, ♀♀, pp $T \geq B \geq A \geq S$, ♂♂ $T \geq A$. Therefore the high percentage visits to Euphorbiaceae, Labiatae, Rosaceae and Borraginaceae determine the higher relative visit of Apidae to non Compositae. However, marked contrasts are seen between B and S, that is, $S > B$ in Euphorbiaceae, Saxifragaceae and Rosaceae and $B > S$ in Labiatae and Borraginaceae.

4) Between ♀♀ and pp, pp > ♀♀ is found in Saxifragaceae (S), and Labiatae (T) and ♀♀ > pp in total Compositae (B), *Senecio* (T, B) and Euphorbiaceae (T, S). Between ♂♂ and ♀♀ or pp, $T \delta > T p$, $B \delta > B p$ in total Compositae, $B \delta > B p$ in *Senecio*, $A \delta > A p > A \delta$ and $S \delta > S p$ in Euphorbiaceae, $A \delta \geq A p \geq A \delta$ in Labiatae, $A \delta > A p > A \delta$ in Rosaceae and $A \delta > a \delta$ in Xyridaceae. Some of these instances may reflect the difference in pollen and nectar intake with respect to the plant groups concerned.

5) No significant difference is noticed between total bumblebees and *B. bellicosus*

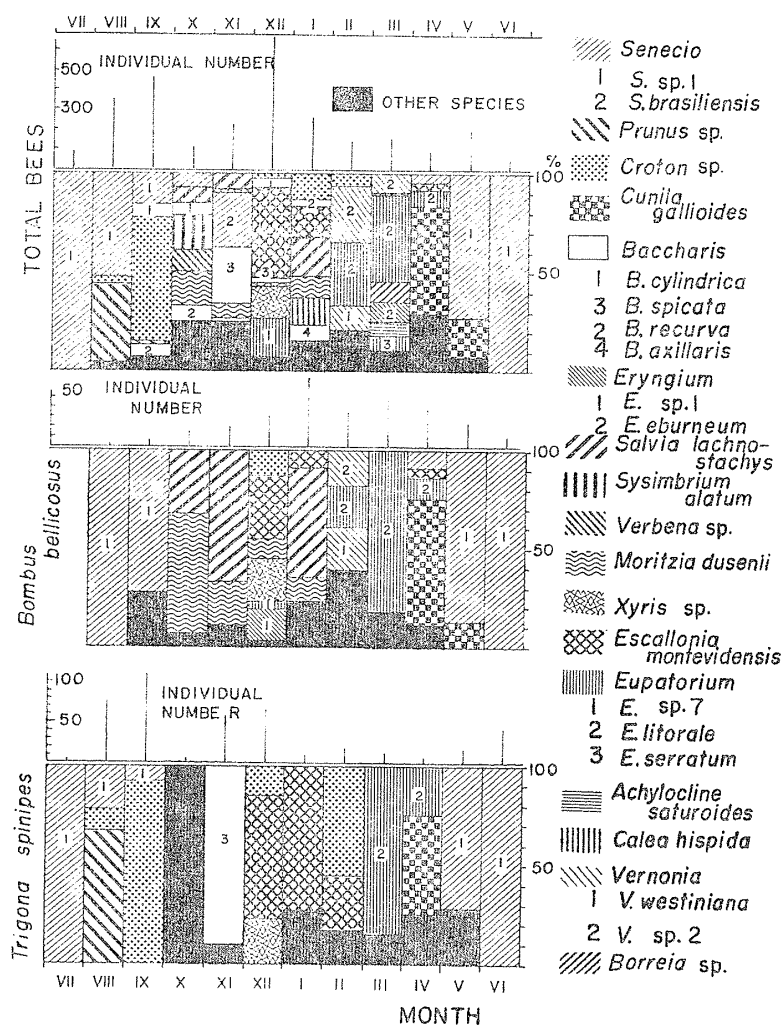


Fig. 4. Phenology of flowers predominantly visited by females of all wild bees, *Bombus bellicosus* and *Trigona spinipes* at SJP, shown by percentage ratios of relative numbers of visits in each month, together with number of individuals collected on flowers.

both in ♀♀ and pp. A slight insignificant difference is observed only in "other genera" of Compositae. Therefore, it is inferred that no particular difference in relative flower visit exists between *B. bellicosus* and *B. atratus*.

Fig. 4 gives the phenology of relative visits in total wild bees, *B. bellicosus* and *T. spinipes*, all females alone, at SJP. Obviously the number of frequently visited flower species must decrease when any particular species is compared to total wild bees, even if the former is quite polytrophic. But some deviations given in the figure cannot be explained by such mere statistical outcome. The high preference for *Salvia lachnostachys*, *Moritzia dusenii* and disregard for *Prunus* sp. 1, *Senecio brasiliensis*, *Baccharis spicata* by *B. bellicosus* is obvious together with the high preference for *Croton* sp., *Baccharis spicata*, *Escallonia montevidensis* and disregard for *Salvia lachnostachys* and *Senecio brasiliensis* by *T. spinipes*. Thus these two dominant apid species behave quite differently as to relative flower visits.

However, one must be cautious to attribute all such differences to innate differences in flower preference, because the results obtained at BV show some remarkable discrepancies from those at SJP. In this case, too, the percentage flower visits with fiducial limits to various plant groups were calculated. For simplicity here are given only some main trends in females:

1) Percentage visit to Compositae is in ♀♀ $B \geq T \geq A \geq S$ and $B > S$, in pp $S \geq A > b$. Compositae > non Compositae is seen in ♀♀ and pp of T, A, B and S, i.e., the overwhelming majority of visits to Compositae is common to all assemblages compared.

2) Within Compositae the following tendencies are observed: *Senecio*, ♀♀ $T > S \geq A \geq B$, pp $S \geq A > b$; *Eupatorium*, ♀♀ $T \geq B \geq A \geq S$, pp $S \geq A \geq b$; *Baccharis*, ♀♀ $S \geq A > T > b$, pp $S \geq A \geq b$; *Vernonia*, ♀♀ $B > A \geq S > T$, pp $B > A \geq S$; other genera ♀♀ $T > S > A > b$, pp $T > b \geq a \geq s$. The relative avoidance of *Senecio* by A, and relation of B and S to *Baccharis* is the same as at SJP while *Eupatorium* is visited by four assemblages without significant difference. *Vernonia* spp., notably *V. westiniana*, are important food sources at BV.

3) Among non Compositae, the following tendencies are observed: Umbelliferae, $S \geq A \geq T > b$, Solanaceae, $S \geq A \geq T \geq B$, Labiatae $S \geq A \geq T > b$, Leguminosae $S \geq A \geq B \geq T$ and $S \geq A > T$, other families $T \geq B \geq A \geq S$ and $T > A \geq S$. The results show floral differences between BV and SJP with respect to frequently visited flowers. The absence of visits to Labiatae by bumblebees is noteworthy. The visits of *B. atratus* were focused on *Vernonia westiniana* in January to March, this plant providing 85% of the flower records of *B. atratus*, nevertheless a labiate species, *Hyptis* sp. 1, was in bloom in the same period.

4) A difference between ♀♀ and pp is seen only on *Baccharis* ($S♀ > Sp$).

5) Between S and *T. spinipes* (TS) the following significant differences are observed: Total Compositae, ♀♀, pp $S > TS$; *Baccharis*, ♀♀ $TS > S$, *Vernonia*, ♀♀, pp $S > TS$, non Compositae, ♀♀, pp $TS > S$, Solanaceae ♀♀, pp $TS > S$ and Leguminosae ♀♀, pp $TS > S$. The differences are mainly caused by the preference by *M. q. quadrifasciata*, *P. quadripunctata* for *Vernonia westiniana*, and nearly complete ignorance to this plant by *T. spinipes*.

6) The flower records of *T. spinipes* are given chronologically as follows (Number of specimens in parentheses): September, *Senecio oleosus* (13), *Allophylus petiolatus* (4); October, *Cestrum corymbosum* (23), *Cassia laevigata* (15); November, *C. laevigata* (4), *Senecio brasiliensis* (1), *Myrcia larvotteana* (3); *Palicourea* sp. 1 (14), *Salvia paranaensis* (7); December, *S. paranaensis* (8); January, *Baccharis* sp. 2 (25); February, *B. sp. 2* (12), *Eryngium eburneum* (8); March, *Vernonia westiniana* (1); April, *Eupatorium* sp. 1 (1); May, Comp., Gen. ? sp. ? (1).

Comparing the results cited above together, it is inferred that, although each apid species shows some preference for particular flower species, it is difficult to regard any of them as oligotrophic. Apparently a specialized oligotrophy is not compatible with their social mode of life and protracted active period. Nevertheless, it is interesting to see their concentration on particular flowers at given periods. This may in part be caused by the

communication system of stingless bees and the wide flight range of bumblebees. The erratic fluctuation in number of individuals of *Tr. spinipes* (Table 1) and the abundance at limited periods of *M. q. quadrifasciata*, *N. bipunctata* and *B. atratus* at BV in spite of the protracted existence of their colonies favor the assumption given above. Probably these bees do not utilize the food sources within their flight areas homogenously, but concentrate their foraging on particular flowers at particular spots. This would result in the limitation of food sources to certain flowers at a given period in spite of a basically polytrophic nature. Thus although an innate preference to some plant groups, for instance, to Labiatae in bumblebees, is probable, this is not so strictly fixed as in some other typically oligotrophic bee groups. Superficial oligotrophy within limited periods could in part be explained by such behavioral plasticity.

Finally a few words are given as to the flower visits by honeybees. We took no systematic records but predominantly visited flowers in certain months were noted as

Table 3. Flower records of the European honeybee, *Apis mellifera*, at SJP and BV.

Month	São José dos Pinhais	Boa Vista
Jul 1	<i>Senecio</i> sp. 1	No record
2	" , <i>Ulex europaeus</i> *	"
3	" , "	"
Aug 1	" (n, p), " (n, p)*
2	<i>Ulex europaeus</i> (n, p)*
3	"	<i>Senecio oleosus</i> (p)
Sep 1	" (n, p)*	" (")
2	" (" , ")*	" , <i>Baccharis elaeagnoides</i> *
3	Various flowers	<i>Allophylus petiolatus</i> *, and flowers of high trees
Oct 1	"	<i>S. oleosus</i> (few), <i>Baccharis</i> sp. 1 (many)*
2	<i>Baccharis erioclada</i> * (virtually	<i>Rhamnus sectipetala</i> (p)*
3	" (") monopolizing)	<i>Senecio brasiliensis</i> (p)
Nov 1	" (")	" (many), <i>R. sectipetala</i> (a few, p)
2	<i>Senecio brasiliensis</i>	<i>Cuphea mesostemon</i> (many, p) <i>R. sectipetala</i> (p, a few)
3	<i>Rhamnus sectipetala</i> *, etc.	<i>Eupatorium serratum</i> (p). <i>S. brasiliensis</i> (p, a few)
Dec 1	<i>Eupatorium</i> sp. 2, <i>E.</i> sp. 7	" ("), " (")
2	No record	No record
3	"	"
Jan 1	"	<i>C. mesostemon</i> , <i>Jussiaea sericeae</i>
2	"	<i>Baccharis</i> sp. 2*, <i>Elephantopus mollis</i> *
3	Various flowers	<i>Vernonia westiniana</i> , <i>C. mesostemon</i>
Feb 1	No record	" , <i>Baccharis</i> sp. 3*, <i>J. sericeae</i> (a few), <i>Hyptis</i> sp. 1 (a few)
2	<i>Eupatorium litorale</i>	<i>Hyptis</i> sp. 1 (n), <i>B.</i> sp. 3 (p, a few), <i>Jungia floribunda</i> (n)*
3	"	<i>Baccharis</i> sp. 2 (p), <i>V. westiniana</i> (a few), <i>Eryngium eburneum</i> (a few)
Mar 1	" , <i>E. serratum</i> *	<i>E. eburneum</i> , <i>V. westiniana</i> (a few), <i>B. anomalus</i> *
2	No record	" (n), <i>Solidago microglossa</i> (p), <i>Eup.</i> sp.
3	"	<i>E.</i> sp.
Apr 1	<i>Cunila gallioides</i>
2	<i>Ulex europaeus</i> *	No record
3	No record	"
May 1	"	No visit
2	<i>Senecio</i> sp. 1	No record
3	"
Jun 1	"	No record
2	" , <i>Ulex europaeus</i> *	"
3	" , " *

Nectar and pollen intake shown by n and p. The distinction was not made for plants without these symbols, * indicates plants not frequently visited by wild bees.

given in Table 3. In general the phenology of preferred flowers coincides with that for other wild bees. But there are some exceptions (indicated by "x") which were relatively disregarded by wild bees but visited by many honeybee workers. The most remarkable species is *Ulex europaeus* at SJP. This introduced plant was the unique representative of Leguminosae in the area and was nearly completely disregarded by wild bees. Virtually only three wild bee individuals, one worker of *B. bellicosus* and two (erroneously given as one in Sakagami, Laroça and Moure 1967a) of *T. spinipes* were captured on this plant. On the other hand, it served for honeybees as one of the principal food sources from late autumn to early spring.

Summary

The relative abundance, phenology and flower visits of apid bees were studied by periodic sampling throughout the year at two grassland areas of Eastern Paraná, Southern Brazil, São José dos Pinhais (SJP) and Boa Vista in Curitiba (BV). Among 10 species collected, *Trigona spinipes* (Fabricius) was the dominant at both areas. *Bombus bellicosus* Smith at SJP and *Melipona q. quadrifasciata* Lepeletier and *Bombus atratus* Franklin at BV were also dominants. The difference in faunal makeup between two areas probably in part depends on the difference in vegetation. The phenology of bumblebees resembled basically that of north temperate species, but the active period was much longer. Bumblebees were collected in each month except July, and possible survival of some colonies in winter was not excluded. The phenology of stingless bees was characterized by erratic fluctuation, suggesting their relative independence from seasons and areas surveyed. Honeybees were active throughout the year. The relative numbers of flower visits of all wild bees and Apidae and among some groups of the latter showed some significant differences. Some of these differences were inferred as the expression of the plasticity in foraging behavior rather than innate oligotrophy to particular plant groups.

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A REVISION OF THE WORLD SPECIES OF THECOBATHRA (LEPIDOPTERA: YPONOMEUTIDAE)

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In the present paper a taxonomic revision is given of the world species of *Thecobathra* Meyrick, with a key to the species, and the specific relationships are discussed.

The genus *Thecobathra* was erected by Meyrick in 1922 for a new Assamese species, *acroperena* Meyrick. Together with this species, the followig six species were referred by me to *Pseudocalantica* Friese, which is here regarded as a junior synonym of *Thecobathra* Meyrick: *anas* (Stringer), *yasudai* Moriuti, *lambda* Moriuti, *eta* Moriuti, *nakaoi* Moriuti and *kappa* Moriuti. Besides them, three species, *casta* (Meyrick), *delias* (Meyrick) and *argophanes* (Meyrick), are now removed from *Niphonympha* Meyrick to the present genus, and two species, *sororiata* and *nivalis*, are described as new, bringing to twelve the total number of species referable to the genus.

I wish to express my thanks to Prof. S. Ito of our laboratory for his direction and encouragement. My gratitude should be also expressed to the following entomologists and the institutions for providing me with material. The abbreviations enclosed in parentheses are used for the location of specimens: Dr. K. Sattler and Mr. P.E.S. Whalley, both of the British Museum (Natural History), London (BMNH); Prof. S. Issiki, Osaka (ISSK); and Dr. W. Forster and Dr. W. Dierl, both of the Zoologische Sammlung des Bayerischen Staates, München (ZSM). For specimens preserved in the collection of the Entomological Laboratory, University of Osaka Prefecture, Sakai, the abbreviation UOP is used. Last but not least, I am particularly indebted to the authorities of the British Museum (Natural History), London, for allowing me the use of the admirable collection as well as for the financial assistance during my stay in London.

Thecobathra Meyrick

Thecobathra Meyrick, 1922, p. 553. — Fletcher, 1928, p. 21, no. 21; *id.*, 1929, p. 220 — Clarke, 1965, p. 395. Type-species: *Thecobathra acroperena* Meyrick, 1922. Monobasic.

Pseudocalantica Friese, 1960, p. 36–37, n. syn.; *id.*, 1962, p. 303. — Moriuti, 1963, p. 217. Type-species: *Niphonympha anas* Stringer, 1930. Original designation and monobasic.