nidial germination than the serine protease inhibitory extract. However, when assayed against germinated conidia, the extracted protease inhibitor fraction was capable of inhibiting germ tube development. Within 48 h germ tubes treated with the inhibitor extract began to lyse. Whether or not the host protease inhibitors present in hemolymph accumulate on the walls invading germ tubes and cause a similar mycostatic effect under in vivo conditions remains to be tested.

In conclusion, we have detected a complex of protease inhibitor activities in resistant *A. gemmatalis* larvae that were not detected in either susceptible *T. ni* or molting *A. gemmatalis* larvae. A site-specific serine protease inhibitor was isolated from *A. gemmatalis* hemolymph that was deleterious to both the germination of *N. rileyi* conidia and subsequent germ tube development. The results of these studies indicate that the resistance expressed by last instar *A. gemmatalis* larvae to infection by *N. rileyi* may in part be due to the presence of hemolymph-borne protease inhibitors that act on fungal hydrolases responsible for continued cell wall development.

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1 Ignoffo, C. M., in: Microbial Control of Pests and Plant Disease, 1970–1980. Academic Press, 1981.
2 Ignoffo, C. M., Puttler, B., Hostetter, D. L., and Dickerson, W. A., J. Invert. Path. *28* (1976) 259.
3 Boucias, D. G., and Pendland, J. C., J. Invert. Path. *38* (1982) 338.
4 Ignoffo, C. M., Garcia, C., and Kroka, M. J., J. Invert. Path. *39* (1982) 198.
5 Kucera, M., J. Invert. Path. *35* (1980) 304.
6 Kucera, M., J. Invert. Path. *38* (1982) 33.
7 Kucera, M., Sehnal, F., and Mala, J., Comp. Biochem. Physiol. 79B (1984) 255.
8 Eguchi, M., Appl. Ent. Zool. *17* (1982) 589.
9 Eguchi, M., Ueda, K., and Yamashita, M., Biochem. Genet. *22* (1984) 1093.
10 Soderhall, K., Devl comp. Immun. *6* (1982) 601.
11 Soderhall, K., Comp. Biochem. Physiol. *74B* (1982) 221.
12 Armstrong, P. B., and Guigley, J. P., Biochim. biophys. Acta *827* (1985) 453.
13 Eguchi, M., Hareda, J., and Iwamato, A., Comp. Biochem. Physiol. *71B* (1982) 569.
14 Sasaki, T., J. Biochem. *84* (1978) 267.
15 Sasaki, T., and Kobayashi, K., J. Biochem. *95* (1984) 1009.
16 Hall, L., and Soderhall, K., J. Invert. Path. *39* (1982) 29.
17 Hall, L., and Soderhall, K., Comp. Biochem. Physiol. *76B* (1983) 699.
18 Armstrong, P. B., Rossner, M. T., and Quigley, J. P., J. expl Zool. *236* (1985) 1.
19 Sugimoto, Y., Hanada, S., Kogo, K., and Sakaguchi, B., Biochim. biophys. Acta *788* (1984) 117.
20 Bradford, M. M., Analyt. Biochem. *72* (1976) 248.
21 Pendland, J. C., and Boucias, D. G., Devl comp. Immun. *43* (1985) 285.

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Ascorbic acid content of neotropical plant parts available to wild monkeys and bats

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Summary. The ascorbic acid content of foliage available to wild primates and bats in Panama (in transition between wet and dry seasons) was lower than that of temperate zone foliage but higher than that of most fruits and vegetables. Intakes of ascorbic acid (mg/kg b.wt/day) by wild primates and frugivorous bats in Panama are much greater than that of most human populations.
Key words. Ascorbic acid; neotropical plants; vitamin C; primates; anthropoids; bats; monkeys.

L-ascorbic acid plays essential roles in several physiological functions in mammals[1]; one of the most important is hydroxylation of collagen, an essential protein of connective tissue. In deficiency of ascorbic acid, collagen is not laid down correctly and scurvy develops. Many species of mammals synthesize their ascorbate requirements[2,3]. Some, however, are unable to do so and are scurvy-prone because they lack the enzyme L-gulonolactone oxidase (GLO, EC 1.1.3.8), which catalyzes the final step in ascorbate synthesis from glucose[4]. To date 12 species of anthropoid primates[5–9], 45 species of bats[10], and the guinea pig[6–8,11] have been categorized as scurvy-prone on the basis of nutritional studies or assays for GLO or both. Anthropoids are here considered to include the families Cebidae, Callitrichidae, Cercopithecidae, Pongidae, and Hominidae. No species of anthropoid primate or bat yet examined has been found to synthesize L-ascorbic acid; all are thought to require a dependable dietary supply of it[12].

Apparently mutations resulting in the loss of GLO occurred on several occasions in mammalian evolution; these mutations appear to be fixed in several taxa. In man, African green monkey, and guinea pig the gene coding for GLO is not expressed[4], but neither the nature nor the site of the mutation is known. Bats have not been checked for expression of the gene. There is no present evidence that the level of dietary ascorbate directly influenced the mechanisms of mutation or fixation, but certainly a mutation resulting in loss of ability to synthesize ascorbate could not persist or be fixed in a population lacking an adequate and regular dietary supply[4,12].

Anthropoid primates probably evolved in a tropical forest environment[13,14]; even today most tropical anthropoid species are arboreal. Plant foods available to anthropoids for most or all of their evolutionary history have been leaves, fruit and flowers of tropical forest trees and vines[14]. All anthropoids routinely include plant foods in the daily diet and most species are estimated to take $\geq 70\%$ of their annual diet from plants[15]. Likewise, many species of bats secure much of their nutrition from plant materials including flowers, nectar, pollen and fruit[16,17]. Many anthropoid primates and several species of bats tend to focus considerable feeding time on members of the family Moraceae, particularly species of the genus *Ficus*[14,16–20].

It would be expected that the tropical plant foods consumed by bats and wild primates would be relatively rich in ascorbic acid but few data are available. In this paper we report ascorbic acid contents of plant samples collected from a Neotropical forest site inhabited by five anthropoid species (*Alouatta palliata, Ateles geoffroyi, Cebus capucinus, Aotus trivirgatus* and *Saguinus oedipus geoffroyi*) and by a number of species of phyllostomid bats including members of the genera *Artibeus, Carollia, Sturnira* and *Glossophaga*. Because *Ficus* species are of particular importance in the diets of these animals, a special effort was made to analyze leaves and fruits of this genus.

Materials and methods. Plant samples were collected from trees

Table 1. Ascorbic acid content of foliage from Barro Colorado

Family, species	Eaten by bats or primates	Tree	Status*	Type**	Ascorbic acid (mg/100g) Fresh	Dry
Moraceae						
Ficus yoponensis	+	41	VY	GS	585	2340
		32	M	GS	67	203
		15	M	GS	132	407
		15	M	SB	84	266
		5	M	GS	79	238
F. insipida	+	31	M	GS	57	136
F. nymphaefolia	+	11	Y	GS	20	104
		20	Y	GS	20	77
F. obtusifolia	+	10	Y	GS	52	260
F. pertusa	+	12		GS	15	46
Cecropia insignis	+	9	VY	SL	58	207
		9	Y	SL	50	178
		9	M	SL	113	269
		9	M	SL	68	179
		17	VY	SL	27	173
		17	Y	SL	80	286
		17	I	SL	96	261
		17	M	SL	101	213
Poulsenia armata		21	M	GS	66	136
		21	M	GS	22	58
		21	M	GS	12	34
		34	M	GS	72	118
Leguminosae						
Platypodium elegans	+	4	M	GS	140	310
		4	M	GS	212	469
		4	M	SB	187	415
		4	M	SB	165	365
		19	M	GS	112	264
Inga fagifolia	+	22	Y	GS	60	190
		22	M	GS	73	138
Ormosia coccinea	+	16	Y	GS	85	266
Bombacaceae						
Ceiba pentandra		43	Y	GS	78	304
		14	I	GS	68	218
Ochroma pyramidale		7	M	GS	108	179
		8	M	GS	176	299
Burseraceae						
Tetragastris panamensis	+	37	VY	GS	76	200
		37	VY	SB	113	170
Anacardiaceae						
Anacardium excelsum		18	Y	GS	120	411
		18	Y	SB	113	409
Bignoniaceae						
Phryganocydia corymbusa	+	23	M	GS	113	211
Piperaceae						
Piper aequale		28	M	GS	7	61

*VY = very young; Y = young; I = intermediate; M = mature; **GS = grab sample from several branches; SB = grab sample from single branch; SL = single leaf.

growing in the moist, lowland tropical forest on Barro Colorado Island, Republic of Panama. A complete description of this forest and of climatic conditions in the geographical region can be found elsewhere[14,21,22]. All collections were made in January (1985) a month that marks the transition between the long (circa 7 months) rainy season and the shorter (circa 3 months) dry season[22]. Most samples were from trees ≥ 25 m in height. Some had been freshly dropped to the ground by monkeys or other mammals feeding in the tree; others were obtained by shooting at branches with large shot. In a few cases (i.e. *Piper, Coussarea, Quassia*), samples were hand-picked from low trees. All samples were sealed immediately in plastic bags, transported to a freezer within 30 min, and kept frozen until analyzed. They were packed in dry ice for transport from Panama to Berkeley, CA and again for transport from Berkeley to Holloman AFB, NM.

Dry matter contents were determined by oven drying 2.5-g portions at 80 °C overnight. Ascorbic acid contents were determined on undried samples with the 2,4-dinitrophenylhydrazine (DNPH) method previously used for foliage of eucalypts and conifers[23]. This method includes both L-ascorbic acid and dehydroascorbic acid, thus total vitamin C.

Results. Total vitamin C contents of the specimens analyzed (expressed as mg ascorbic acid per 100 g on both fresh and dry weight bases) are summarized in tables 1 and 2. Plant parts known to be eaten by monkeys and/or bats are specifically designated. All samples contained ascorbate but concentrations varied considerably among plant parts, individual plants, and species. In general, foliage had a higher ascorbate content than flowers or fruits, particularly ripe fruits. Immature foliage and fruits tended to have higher ascorbate contents than mature foliage and fruits, respectively. The few flower samples analyzed indicate that flowers may have higher ascorbate concentrations than ripe fruit.

In a few cases samples of foliage taken from the same tree varied considerably in ascorbate content. In one case, *Poulsenia armata*, two foliage samples from branches 30 m above the ground (2 individuals) had considerably higher concentrations of ascorbate than two taken 4–5 m above the ground (1 individual) suggesting that greater exposure to sunlight and possibly faster growth or metabolism may increase ascorbate content. The highest ascorbate contents were found in young leaves (585 mg/100 g) and unripe fruit (268 mg/100 g) of *Ficus yoponensis*.

Discussion. Our data for Neotropical angiosperms are compared with those for both tropical and temperate angiosperms in table 3. The range of ascorbate content of foliage from Panama is somewhat wider and the mean somewhat lower than reported for several species from Venezuela[24], Wales (Britain)[25] or New South Wales (Australia)[23]. Likewise the ascorbate content of fruits from Panama averages somewhat lower than reported for 11 tropical fruits in Nigeria[26] or 4 in Venezuela[24]. Fruits generally contain less ascorbate than foliage[24], but a few fruits have extremely high contents; a tropical plum *(Terminalia ferdinandina)* of Australia had 2300–3150 mg/100 g[27] and the West Indian Cherry *(Malpighia punicifolia)* 577–2330 mg/100 g[28,29]. None of the fruits analyzed by us approached such high ascorbate contents. Our data are for samples collected in the transition period between wet and dry seasons. Possible seasonal variations in ascorbate content, as observed in temperate angiosperms and conifers[23], remain to be defined.

Of the five species of primates on Barro Colorado, the spider monkey, *Ateles geoffroyi*, has been shown to lack GLO[8]. The cottontop tamarin (probably *Saguinus oedipus oedipus*) a close relative of the *Saguinus oedipus geoffroyi* of Barro Colorado also lacks GLO[30] and *Cebus fatuellus (C. apella)*, congeneric with *C. capucinus* of Barro Colorado, developed scurvy on an ascorbate-free diet[31]. Furthermore, because all 12 species in 9 genera of anthropoids so far examined[4–9] lack GLO and/or require dietary vitamin C, it is probable that all five species on Barro Colorado share this characteristic. Daily dietary requirements have not, however, been defined adequately for any primate species other than *Homo sapiens*. Intakes from less than 1 to more than 10 mg/kg b.wt/day have been reported as necessary to prevent scurvy or to maintain blood ascorbate at 'satisfactory levels'[5,12,32]. (Recommended daily allowances for adult humans in the USA are about 1 mg/kg b.wt[33], and in some other countries even less.)

Field observations indicate that a 7-kg wild howler monkey *(Alouatta palliata)* on Barro Colorado may consume 600 g of fruit and 400 g of foliage per day[34]. If these have the average ascorbate contents given in table 3, intake would be 279 mg from fruit and 334 mg from foliage for a total of 614 mg or 88 mg/kg/day, far in excess of even the highest estimates of the minimum daily requirement of primates. Furthermore, these animals tend to eat more immature than mature leaves[35], and thus their ascorbate intakes may be even higher. Spider monkeys *(Ateles geoffroyi)* are primarily frugivorous, but consume more food and have much faster gut passage rates than howlers[36]. A 7

Table 2. Ascorbic acid content of fruit and flowers

Family, species	Eaten by bats or primates	Tree	Status*	Ascorbic acid mg/100g Fresh	Dry
	Fruit				
Moraceae					
Ficus yoponensis	+	15	U	268	1218
		13	R	87	362
F. insipida	+	27	U	128	492
		27	U	122	525
F. obtusifolia	+	36	R	16	67
F. pertusa	+	12	U	65	316
F. trigonata	+	24	R	16	74
F. costaricana	+	26	R	14	60
Cecropia insignis	+	42	R	56	254
		30	R	14	77
Leguminosae					
Platypodium elegans	+	4	U	33	77
Piperaceae					
Piper aequale	+	28	R	41	270
Rubiaceae					
Coussarea curvigemma	+	25	R	7	22
		38	R	6	20
	Flowers				
Bombacaceae					
Ochroma pyramidale		7	B	34	157
Pseudobombax septenatum	+	40	F	26	214
Simaroubaceae					
Quassia armata		1	F	180	195
		2	F	72	95

*U = Unripe; R = Ripe; B = Bud; F = Flower.

kg spider monkey may consume as much as 1600 g of fruit per day, which would furnish 744 mg of ascorbic acid or 106 mg/kg b.wt/day.

Bourne[37] long ago calculated that wild gorillas may have intakes of ascorbic acid of 4.5 g/day, or 20–30 mg/kg b.wt/day. Jones and Hughes[25] suggested that the ancestral line of *Homo sapiens* probably consumed much more vitamin C than do most contemporary humans. Eaton and Konar[38] calculated that late Paleolithic human diets (35% meat, 65% vegetable) furnished 392 mg ascorbic acid per day (about 6 mg/kg b.wt/day) whereas the current American diet supplies only about 88 mg/day (1.5 mg/kg b.wt/day). Our results support these views. Present day anthropoids (and by analogy extinct anthropoids) in tropical forests have available ample vitamin C which they routinely consume in amounts per kg of body mass that are much higher than estimated minimum requirements for humans.

Twelve species of herbivorous bats (in 8 genera in the family Phyllostomidae) have been found to lack GLO[10] and thus to require dietary vitamin C. Most or all of these may be found on Barro Colorado. Some eat primarily fruit; none eat much foliage[16,17]. An *Artibeus jamaicensis* weighing 45 g and eating 25 g of unripe fruit containing 46.5 mg of ascorbate/100 g would obtain 12 mg of ascorbate or 258 mg/kg b.wt/day. Minimum daily requirements for bats have not been established, but it seems reasonable to conclude that such a large intake is more than sufficient.

The significance of the high intakes of ascorbate by tropical primates and bats cannot be evaluated properly until more is known of its fate and metabolism in these animals. Specifically rates and pathways of metabolism and excretion and size of body pools need to be elucidated.

In man and guinea pig, a deficiency of vitamin C diminishes the ability to detoxify potentially toxic compounds such as phenolics and terpenoids[39]. These compounds occur routinely in wild plant parts, are prevalent in tropical foliage and are often viewed as deterrents of herbivores[35,40]. Thus, rather paradoxically, tropical foliage (and other plant parts) often provide the animal consumer with the ascorbate needed to aid in the efficient detoxification of some compounds regarded as defenses against herbivore predation. Of course, the coincidence of high levels of ascorbate and phenolics and terpenoids in some plants must have evolved as a result of functions beneficial to the plants, not to increase the utilization of plants by animals. Unfortunately little is known of the functions and metabolism of any of these compounds in plants. In fact, the functions and metabolism of L-ascorbic acid in plants is little known except that it is a precursor of oxalate or tartrate in certain species[41].

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Table 3. Ascorbic acid content of angiosperms from different locales

Locale, kind of samples	No. Species	No. Specimens	Ascorbic Acid (mg/100 g fresh wt) Mean*	SD	Median	Range	Ref.
Panama							
Foliage	16	40	96.3	92.6	78	7–585	This paper
Foliage**	16	39	83.8	48.6	76	7–212	This paper
Fruit	10	14	62.4	72.0	37	6–268	This paper
Fruit***	10	13	46.5	42.6	33	6–128	This paper
Flowers	3	4				16–180	This paper
Venezuela							
Foliage****	4		197.5	86.1		119–300	24
Fruit juice****	4		85.0	32.6		55–118	24
Nigeria							
Fruit unusual	10		81.7	81.9		12–260	26
Fruit common	8		73.6	88.5		17–289	26
Wales (U.K.)							
Foliage	213	ca. 2500	161.7	109.4			25
New South Wales (Australia)							
Foliage (evergreen)	10	10	198.3	81.8		102–307	23
Foliar cultivars	10		57.3	26.2			25
Plant food of hunter-gatherers	27		26.8				38

*Mean of all specimens for Panama material, mean of species for others. **Very young leaves of *F. yoponensis* excluded; ***Unripe fruit of *F. yoponensis* excluded; ****Lemon, orange, mango, papaya.

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1 Counsell, J.N., and Hornig, D.H., Vitamin C (Ascorbic Acid). Applied Science Publishers, London 1981.
2 Chatterjee, I.B., Science *182* (1973) 1271.
3 Jenness, R., Birney, E.C., and Ayaz, K.L., Comp. Biochem. Physiol. *67B* (1980) 195.
4 Sato, P., and Udenfriend, S., Vit. Horm. *36* (1978) 33.
5 Day, P.L., Vit. Horm. *2* (1944) 71.
6 Grollman, A.P., and Lehninger, A.L., Archs Biochem. Biophys. *69* (1957) 458.
7 Burns, J.J., Nature *180* (1957) 553.
8 Nakajima, Y., Shantha, T.R., and Bourne, G.H., Histochemie *18* (1969) 293.
9 De Klerk, W.A., Kotze, J.P., Weight, M.J., Menne, I.V., Matthews, A., and McDonald, T., S. Afr. med. J. *47* (1973) 1503.
10 Birney, E.C., Jenness, R., and Ayaz, K.M., Nature *260* (1976) 626 and unpublished data.
11 Collins, M., and Elvehjem, C.A., J. Nutr. *64* (1958) 503.
12 Tillotson, J.A., and O'Connor, R., Int. J. Vit. Nutr. Res. *50* (1980) 171.
13 Jolly, A., The Evolution of Primate Behavior. Macmillan Pub. Co., New York 1985.
14 Milton, K., The Foraging Strategy of Howler Monkeys: A Study in primate Economics. Columbia University Press, New York 1980.
15 Clutton-Brock, T.H., and Harvey, P.H., Species differences in feeding and ranging behavior in primates, in: Primate Ecology, p. 557. Ed. T.H. Clutton-Brock. Academic Press, New York 1977.
16 Heithaus, E.R., Fleming, T.H., and Opler, P.A., Ecology *56* (1975) 841.
17 Gardner, A.L., Feeding habits, in: Biology of Bats of the New World Family Phyllostomatidae Part II, p. 293. Eds R.J. Baker, J.K. Jones, Jr and D.C. Carter. Spec. Publ. 13 The Museum, Texas Tech. University, Lubbock, TX 1977.
18 Hladik, C.M., Chimpanzees of Gabon and chimpanzees of Gombe: Some comparative data on the diet, in: Primate Ecology, p. 481. Ed. T.H. Clutton-Brock. Academic Press, New York 1977.
19 Chivers, D.J., Contr. Primatol. *4* (1974) 1.
20 Terborgh, J., Five New World Primates. Princeton University Press, Princeton, NJ 1983.
21 Allee, W.C., Ecology *7* (1926) 273.
22 Leigh, E.G., Rand R.S., and Windsor, D.M. (Eds), The Ecology of a Tropical Forest: Seasonal Rhythms and Long Term Changes. Smithsonian Press, Washington, D.C. 1982.
23 Dash, J.A., and Jenness, R., Experientia *41* (1985) 952.
24 Marquez, V.M., and Baumrucker, J., Acta cient. venezol. *8* (1957) 35.
25 Jones, E., and Hughes, R.E., Phytochemistry *22* (1983) 2493.
26 Keshinro, O.O., Nutr. Rep. Int. *31* (1985) 381.
27 Brand, J.C., Cherikoff, V., Lee, A., and Truswell, A.S., Lancet (1982) 873.
28 Asenjo, C.F., and Moscoso, C.G., Food Res. *15* (1950) 103.
29 Wenkham, N.S., and Miller, C.D., Hawaii Agr. exp. Stat. Bull. *135* (1965) 7.
30 Yess, N.J., and Hegsted, D.M., J. Nutr. *92* (1967) 331.
31 Shaw, J.H., Fedn Proc. *8* (1949) 396.
32 Natl Acad. Sci. (USA) Nutrient Requirements of Domestic Animals, No. 10 2nd rev. edn. Washington, D.C. 1972.
33 Natl Acad. Sci. (USA) Revised Recommended Dietary Allowances, 9th rev. edn. Washington, D.C. 1980.
34 Nagy, K.A., and Milton, K., Ecology *60* (1979) 475.
35 Milton, K., Am. Nat. *114* (1979) 362.
36 Milton, K., Am. Nat. *117* (1981) 496.
37 Bourne, G.H., Br. J. Nutr. *2* (1949) 341.
38 Eaton, S.D., and Konar, M., New Engl. J. med. *312* (1985) 283.
39 Ioannides, C., and Parke, D.V., J. hum. Nutr. *33* (1979) 357.
40 Freeland, W.J., and Janzen, D.H., Am. Nat. *108* (1974) 269.
41 Loewus, F.A., and Helsper, J.P.F.G., in: Ascorbic Acid: Chemistry, Metabolism, and Uses, p. 249. Eds P.A. Seib and B.M. Tolbert. Am. chem. Soc., Washington, D.C. 1982.

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Oviposition stimulants of a *Citrus*-feeding swallowtail butterfly, *Papilio xuthus* L.

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Summary. A methanolic extract of *Citrus unshiu* induces oviposition by females of a *Citrus*-feeding swallowtail butterfly, *Papilio xuthus* L. The chemical factors responsible for stimulating oviposition were isolated and characterized as 5-hydroxy-*Nω*-methyltryptamine, adenosine, vicenin-2, narirutin, hesperidin and rutin. An artificial blend of these six components elicited significant oviposition behavior, apparently identical to that induced by contact with intact *Citrus* leaves.
Key words. Oviposition stimulant; host selection; butterfly; *Papilio xuthus; Citrus;* 5-hydroxy-*Nω*-methyltryptamine; adenosine; flavonoid.

The larvae of most lepidopterous insects feed on a limited number of closely related host plants. The choice of oviposition sites by the adult females is crucial to the survival of their offspring[1,2]. *Papilio xuthus* L. (Papilionidae) is a swallowtail butterfly whose larvae feed exclusively on plants in the family Rutaceae. More than seventy related species in the genus *Papilio* are strongly associated with rutaceous plants[3,4] and many of them are pests of *Citrus* crops. The females lay eggs with great precision on young leaves of their host plants. Alighting on the plants, females vigorously drum upon the leaf surface with their forelegs. After detecting, through their tarsal receptors[5], the specific oviposition stimulants contained in their host plants, the females then lay eggs[5]. The same oviposition behavior can be induced when female butterflies are brought into contact with a piece of filter paper treated with a methanolic extract of their host plants (fig. 1). The oviposition stimulant of *P. xuthus* appeared to be a mixture of highly polar non-volatile compounds[5,6]. We describe here how we were able to resolve the mixture and identify six compounds, the blend of which elicited oviposition behavior apparently identical to that elicited by extracts or intact leaves of *Citrus* plants.

Materials and methods. Leaves of *Citrus unshiu* Marc. (1.2 kg), one of the most common host plants of *P. xuthus*, were extracted with methanol (3 l, by soaking for three months at 5 °C). Gravid females of *P. xuthus* usually responded immediately to the standard methanol extract at a dose of 0.03 g leaf equivalents per 10 cm^2 of filter paper (g.l.e./f.p.) in the behavioral bioassay shown in figure 1. Each female butterfly (hand-paired within 2 days of emergence, 3–10 days old) was introduced into a bioassay chamber ($50 \times 50 \times 50$ cm^3) which is open in front and illuminated by a fluorescent lamp (15 W) at the rear. The test filter paper was brought into contact with the female's forelegs as much as possi-