Is there dimorphism for style lengths in monoecious figs?

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Contrary to the expectation, style lengths of flowers of seven tropical monoecious fig species exhibited normal distribution with a single mode; none of the species showed the expected bimodal distribution. In four of the species studied, nearly 100% of the flowers in a syconium had styles shorter than the mean length of the ovipositor of their pollinator wasp, indicating that the wasps can potentially usurp a greater proportion of the flowers than is generally thought. Thus, our results do not support the belief held for almost three decades that using style length as a strategy, figs can guard their flowers against complete depredation by wasps. The style lengths showed 3–4 times greater variation compared to the ovipositor length of their pollinator wasp. We suggest this to be a consequence of the evolutionary conflict between the fig and the pollinator over the allocation of flowers to wasp production and to seed production.

FOR almost three decades the interaction between figs (*Ficus* spp. Moraceae) and their species-specific pollinating wasps (Agaonidae, Hymenoptera) has been cited as one of the perfect examples of plant–pollinator mutualism[1–3]. The flowers of figs are enclosed in an urn-shaped inflorescence, the syconium. The pollen-laden female wasps enter the receptive syconium through a specialized opening, the oestiole. These wasps can reproduce only within the syconium by ovipositing in the ovaries, on which the wasp larvae feed. It was believed that monoecious figs bear two distinct kinds of female flowers, those with short styles into which wasps can lay eggs and those with long styles into which they cannot as their ovipositor does not reach the ovary; the latter,

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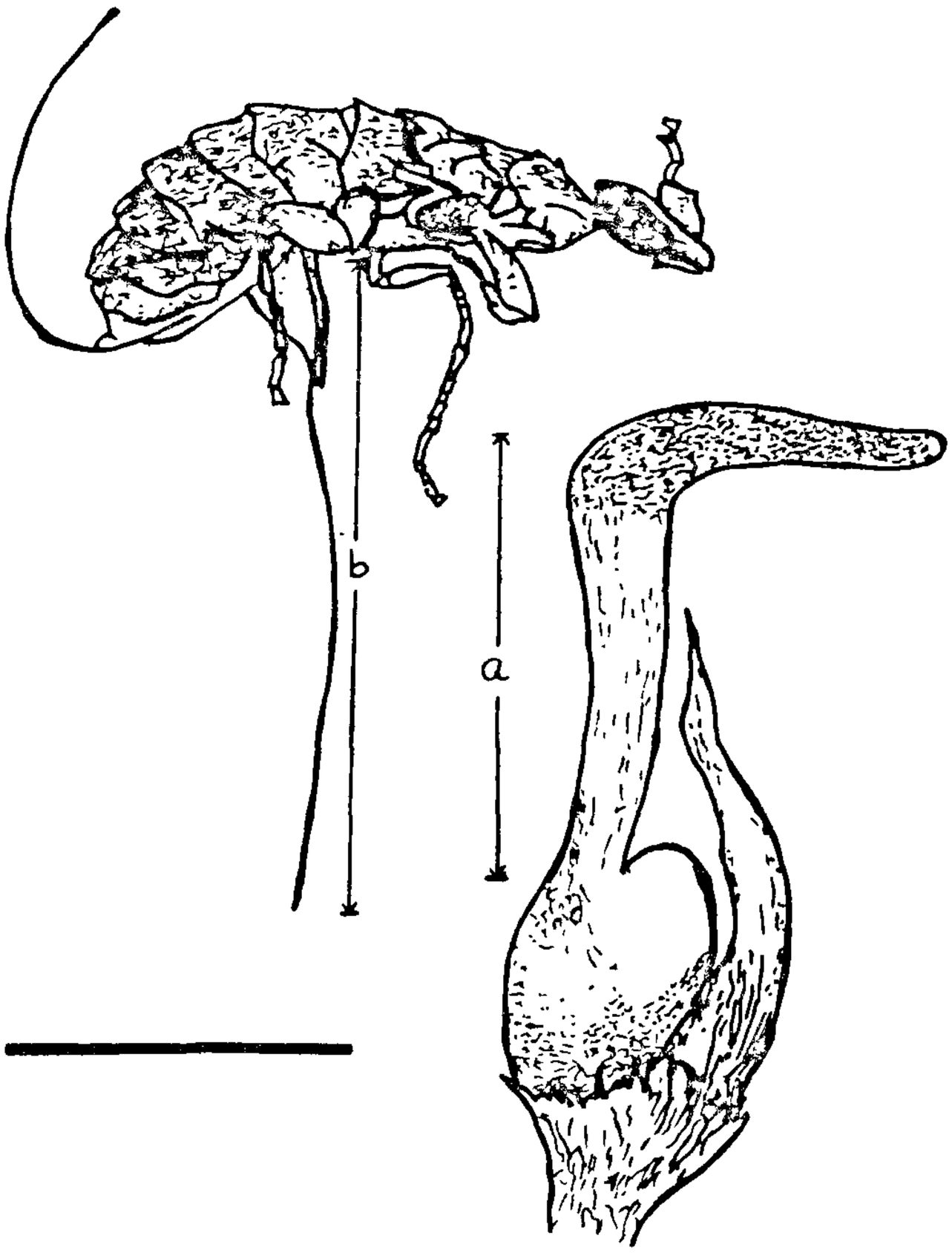

Figure 1. Schematic representation of style length (*a*) and ovipositor length (*b*) measured Bar = 1 mm

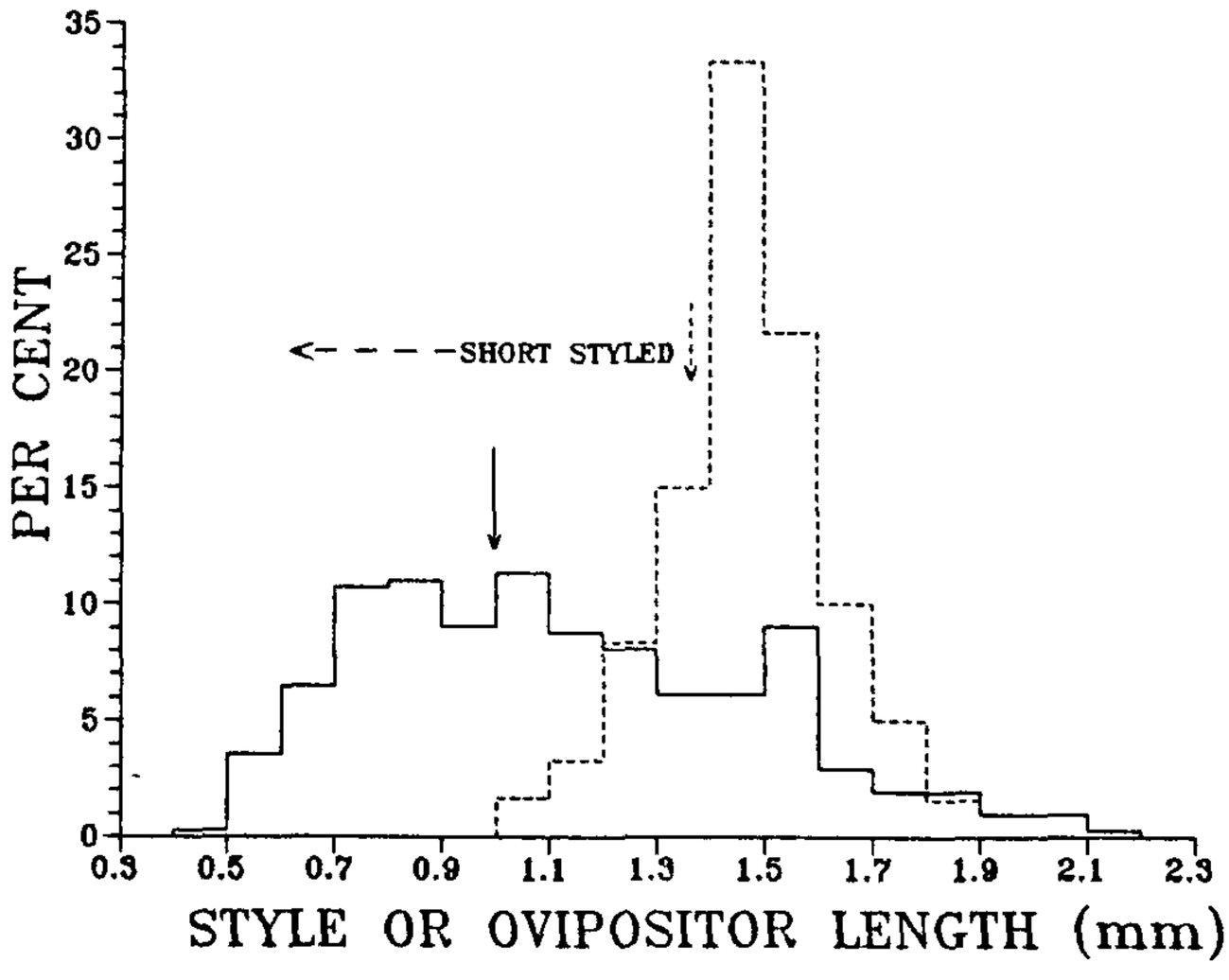

Figure 2. Distribution patterns of style lengths (solid) of *Ficus benghalensis* and ovipositor lengths (dotted) of its pollinating wasps (*Eupristina masoni*) Mean values of the style (solid arrow) and ovipositor (dotted arrow) lengths are also indicated Flowers with style lengths smaller than the mean ovipositor length were considered short-styled

Table 1. Mean style lengths of seven tropical monoecious fig species and the ovipositor lengths of their pollinating wasps*

Fig species	n	Style length (mm) $\bar{x}$	SD	CV (%)	Pollinator wasp species	n	Ovipositor length (mm) $\bar{x}$	SD	CV (%)	Percentage of short-styled flowers†
F. benghalensis L	309	1 027	0 358	34 85	*Eupristina masoni* (Saunders)	60	1 366	0 154	11 27	81 23 (79 09)
F racemosa L	61	1 023	0 222	21 70	*Ceratosolen fusciceps* (Mayr)	50	0 988	0 053	5 36	48 33 (47 17)
F sp.	150	0 723	0 313	43 29	*Platyscapa* sp.	30	1 172	0 042	3 58	93 00 (89.58)
F religiosa L.	218	0 458	0 182	39 74	*Platyscapa quadraticeps* (Mayr)	59	1.047	0 048	4 58	99 08 (99 53)
F. mollis Vahl.	103	0 441	0 140	31 75	*Eupristina* sp.	34	0 415	0 032	7 71	47 58 (45.52)
F. tsjahela Rheede	450	0 394	0 102	25 89	*Waterstoniella keralensis* (Priyadarshan & Abdurahiman)	30	0.758	0.057	7.52	100 00 (100 00)
F drupaceae Thunb	124	0 249	0 084	33 73	*Eupristina belgaumensis* (Joseph)	34	0 553	0 055	9 95	100 00 (99 32)

†The percentage of short-styled flowers was computed as the proportion of flowers with style lengths less than the mean ovipositor length of the respective pollinating wasps. Values in the parentheses indicate percentage of styles that would be shorter than the ovipositor length of any randomly chosen wasp, this was computed by comparing the style lengths of all the flowers sampled with the ovipositor lengths of all the wasps sampled, for a given fig–wasp association

*K–S test indicated good fit ($p > 0.05$) to a normal distribution for all the seven species

hence, produce mature seeds. It is argued that this dimorphism in style lengths apportions the flowers for seed and wasp production[2,4]. The existence of such dimorphism in flowers is expected to lead to bimodal distribution of style lengths. This has frequently been discussed as an important strategy of figs in the context of the cost to be incurred by the fig to raise a seed[5].

Recently, a few studies have questioned the ubiquity of this strategy among figs[6–8]. However, these studies are restricted to one species each, mostly from the neotropics and Africa. Till date there are no comparative studies involving a set of monoecious species to test the existence of stylar dimorphism[9]. In this communication, we report the data for style length distributions of seven tropical monoecious fig species. We discuss our results on the distribution patterns of style lengths and ovipositor lengths in the context of the percentages of flowers available for seed and wasp production.

We measured the length of the style (from the top of the ovary to the base of the stigma) and ovipositor (from the point of attachment to the body to the tip, after separating the sheaths) nearest to 0.01 mm under a microscope (Figure 1). Flowers from at least five receptive (B-phase[1]) syconia and thirty pollinator wasps per species, collected from naturally growing fig trees in and around Bangalore (12°58'N, 77°35'E), India, were sampled for these measurements. As a preliminary test of bimodality, the goodness of fit of the style length to normal distribution was assessed employing the Kolmogorov–Smirnov test[10].

Style lengths of all the seven species showed a continuous distribution; there was no indication of bimodality or the existence of discrete classes of short- and long-styled flowers (Table 1 and Figure 2; distribution patterns of style lengths of *F. benghalensis* and the ovipositor lengths of its pollinating wasps are shown as a representative example). All the species fit well to normal distribution and, hence, the test for bimodality was not attempted. This showed that style lengths of monoecious figs seem to exhibit a unimodal distribution without any distinct group of long- or short-styled flowers. However, it is possible to identify short- and long-styled flowers relative to the length of the ovipositor of the respective pollinating wasp. Surprisingly, this analysis showed that, in four out of the seven species studied, nearly 100% of the styles in syconium were shorter than the mean ovipositor length of their respective wasp, indicating that the pollinators can potentially usurp all the flowers; in *F. benghalensis* more than 80% of the female flowers were accessible to oviposition. These results contradict Murray's suggestion[11] that generally about half the styles are longer than the female wasp's ovipositor. Our results also question the existing belief[4,5,12–15] that figs can guard their flowers against complete depredation by wasps using the style length as a strategy. Thus, the general belief of equal allocation of

flowers[11], based on style lengths, for the production of seeds and wasps does not seem to hold true in monoecious figs[16].

Nevertheless, it is important to note that variation in the style lengths of a species was three to four times more than that in the ovipositor length of their respective pollinator wasps (Table 1). Such variation for style lengths compared to ovipositor lengths has also been reported earlier[6,7]. Though the reason for this difference is not immediately clear, it is not unlikely that selection has favoured greater variance in style lengths as a plant strategy in evolutionary conflict between the fig and the pollinator, on the allocation of flowers to wasp and seed production.

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