Fig trees as keystone species in tropical forests

Next, the trees said to the fig tree, “Come and be our king!”

Old Testament, Judges 9,10

Ficus religiosa:
Buddha sat under its shade for six years

Ficus:

750 species

world-wide

135 species

in New Guinea

Ficus congesta

Ficus wassa

Strangler figs


Photo M. Janda

Banyan fig trees [banian = Hindu merchants who set up markets in the shade of these trees]
Ficus benghalensis


Photo G. Weiblen

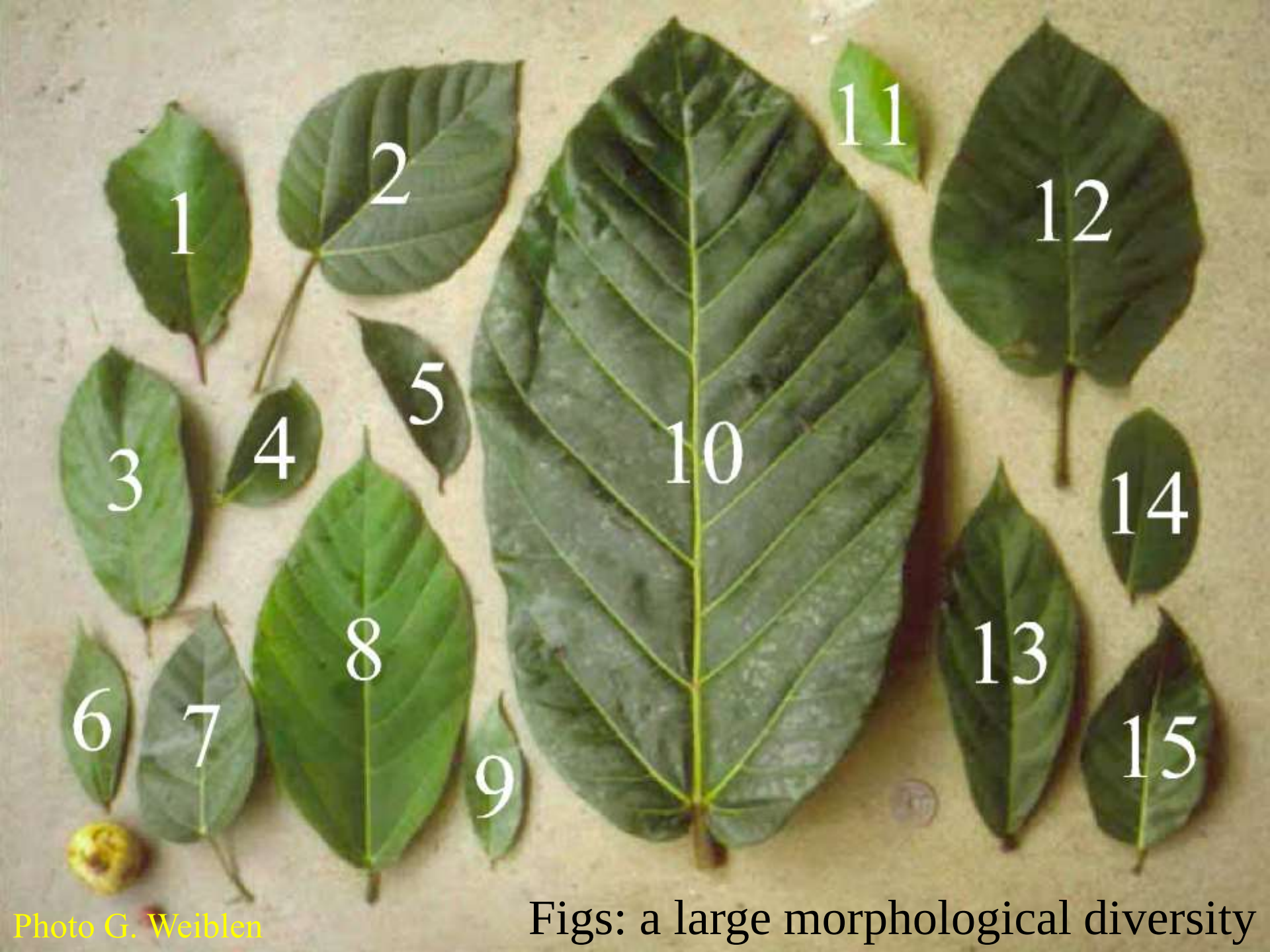


Photo G. Weiblen

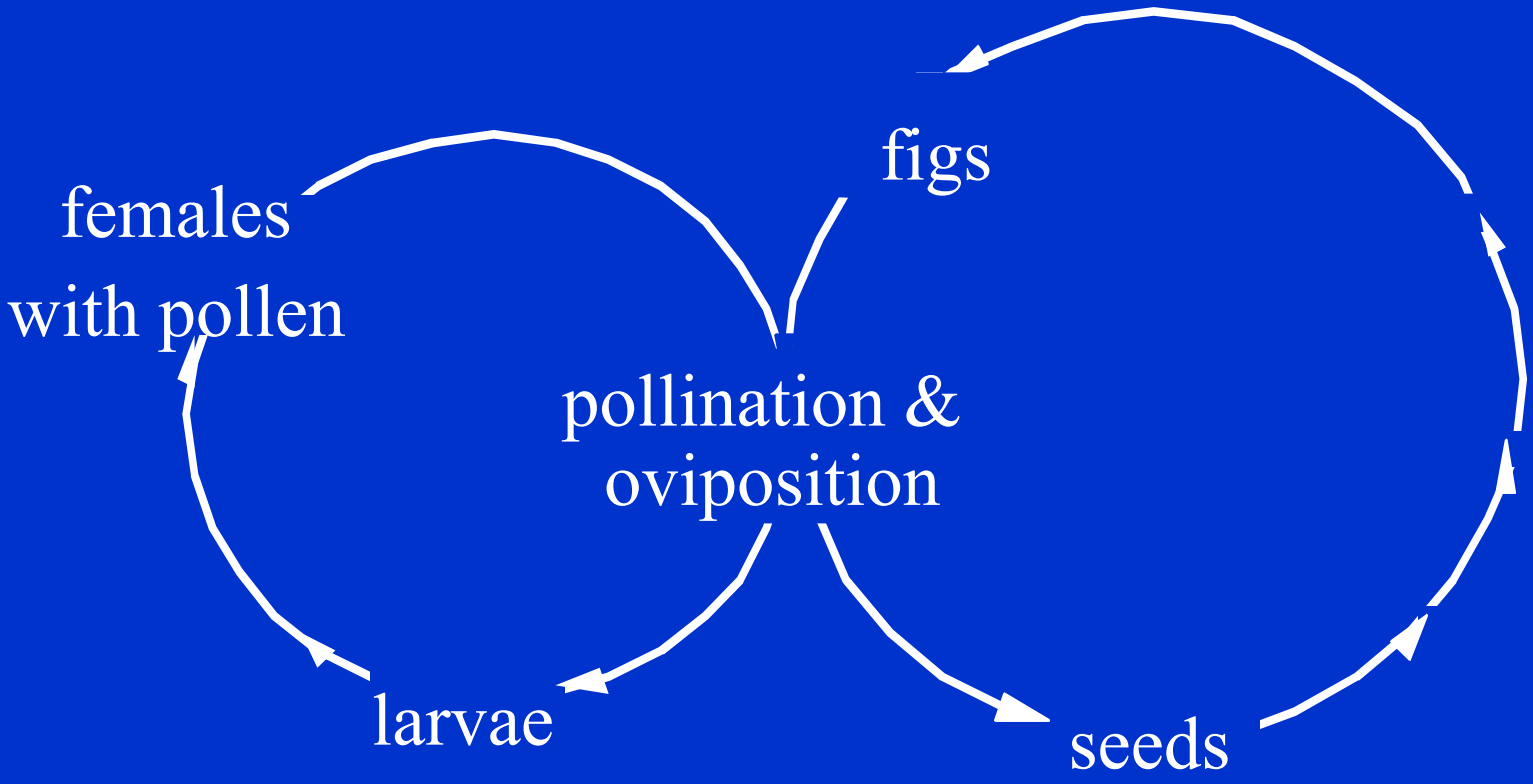
Figs: a large morphological diversity

Ficus trees and their pollinator wasps: why are they in every textbook?

They have a specific mode of pollination relying on a specialised pollinator that also feeds on the seeds produced by the pollination. **Consequences**:

- Ecological diversity: 750 *Ficus* species
- Extreme pollinator specificity
- Resource conflicts with pollinating seed predators
- Parasites on the mutualism
- Aseasonal flowering and fruiting
- High pollen dispersal efficiency
- Keystone resource for frugivores
- High seed dispersal efficiency

Fig wasps and figs: intertwined life cycles



courtesy G. Weiblen

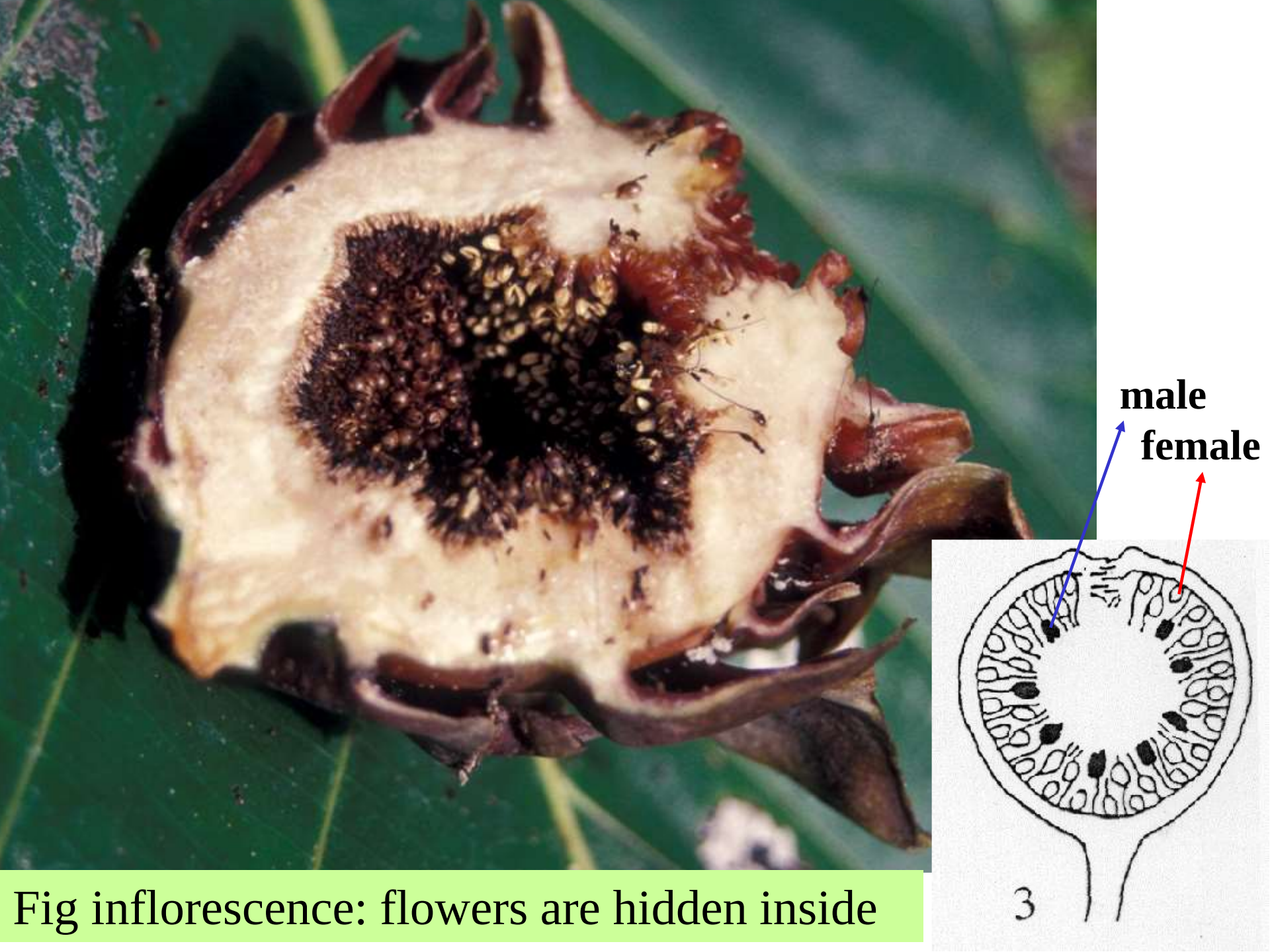


Fig inflorescence: flowers are hidden inside

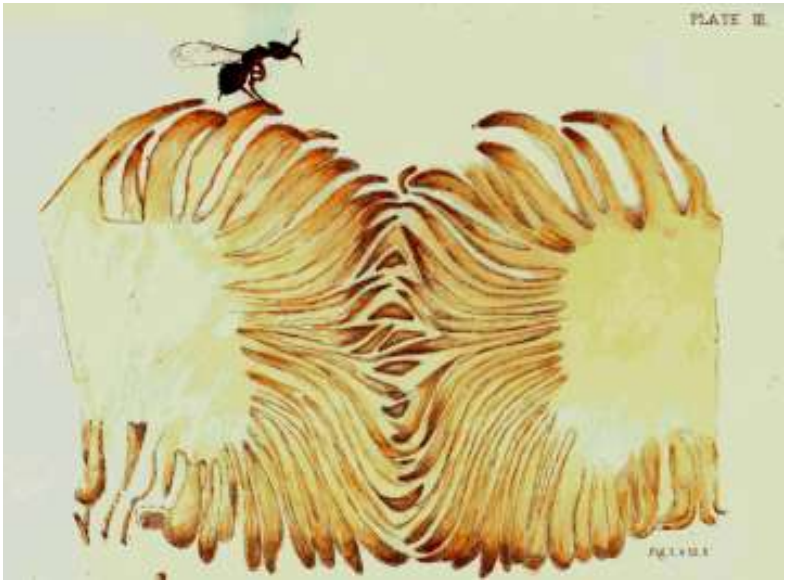
Agaonidae: pollinating fig wasps

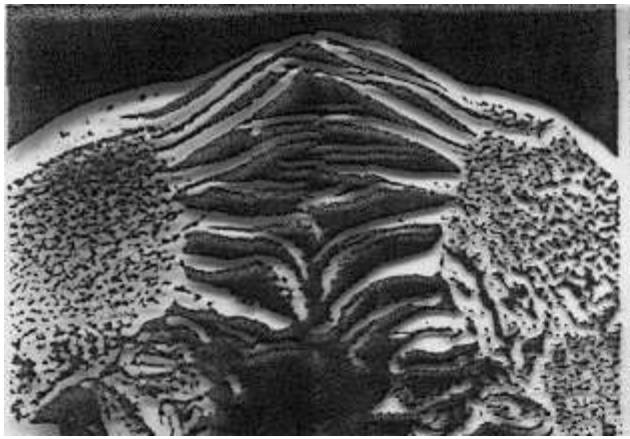
female

male

Photo G. Weiblen

Ostiole - security gate to the flowers





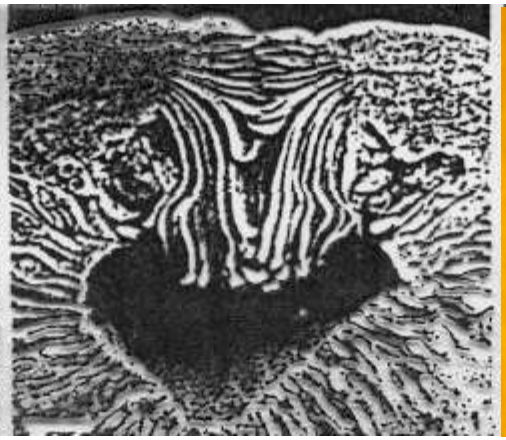


Photo G. Weiblen

Oviposition to fig flowers through stylus

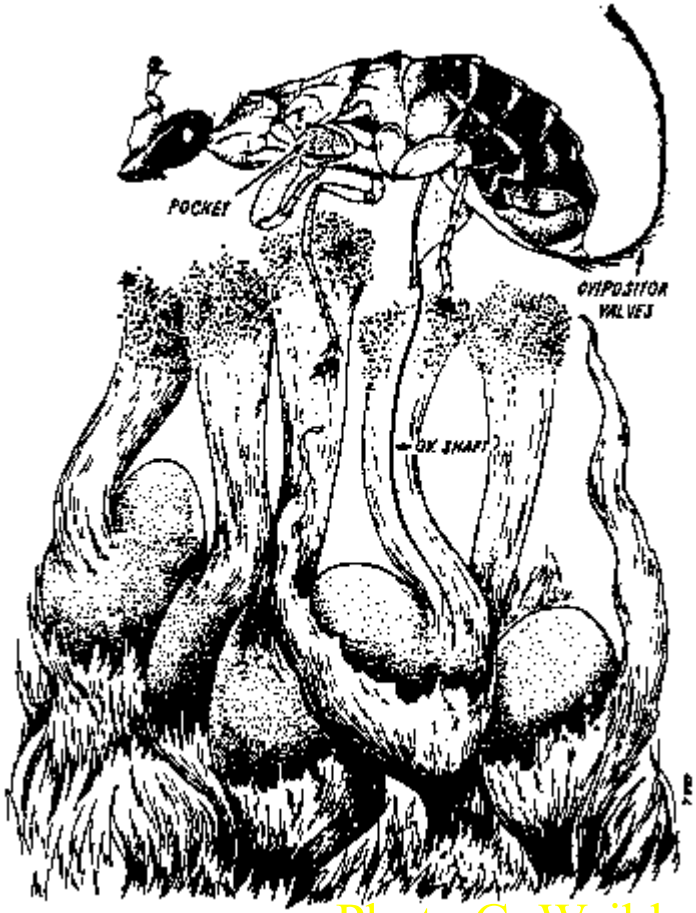
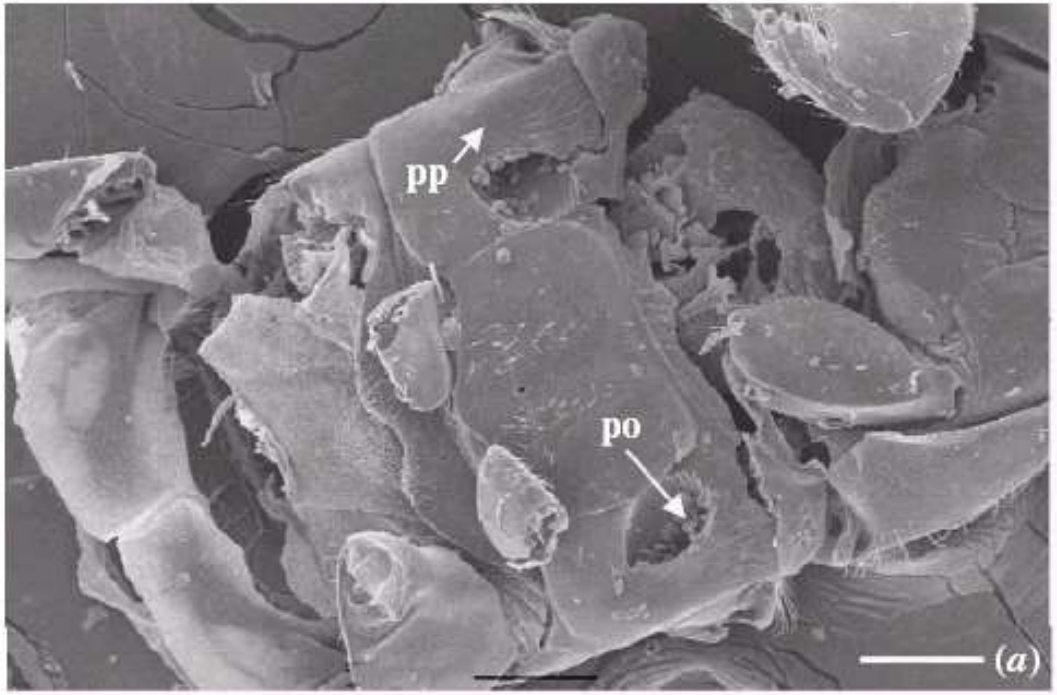
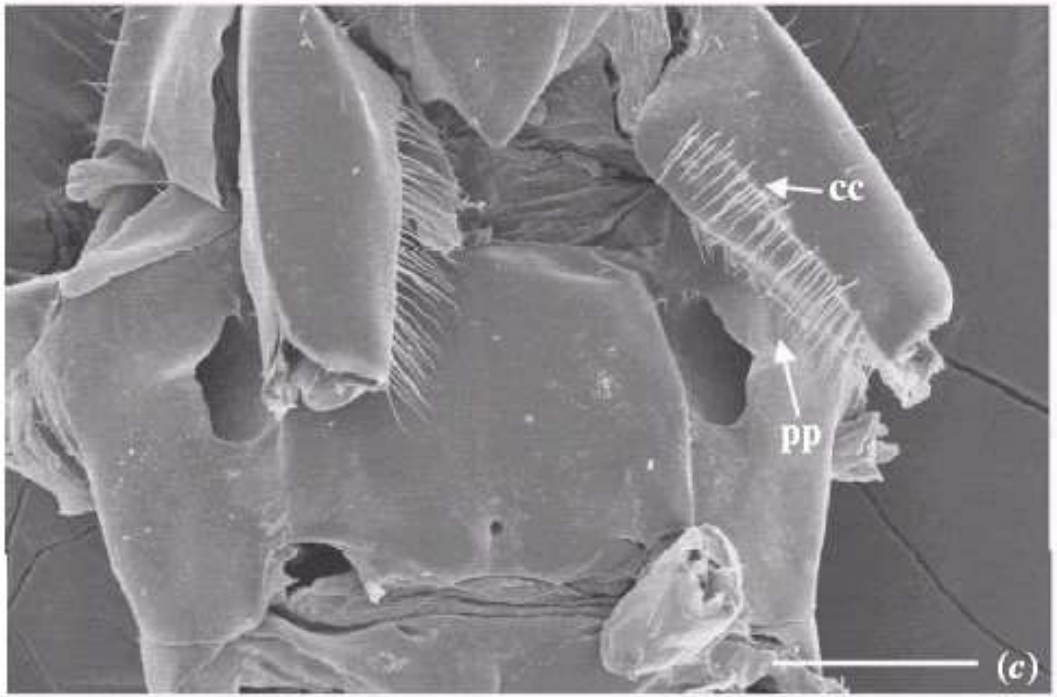


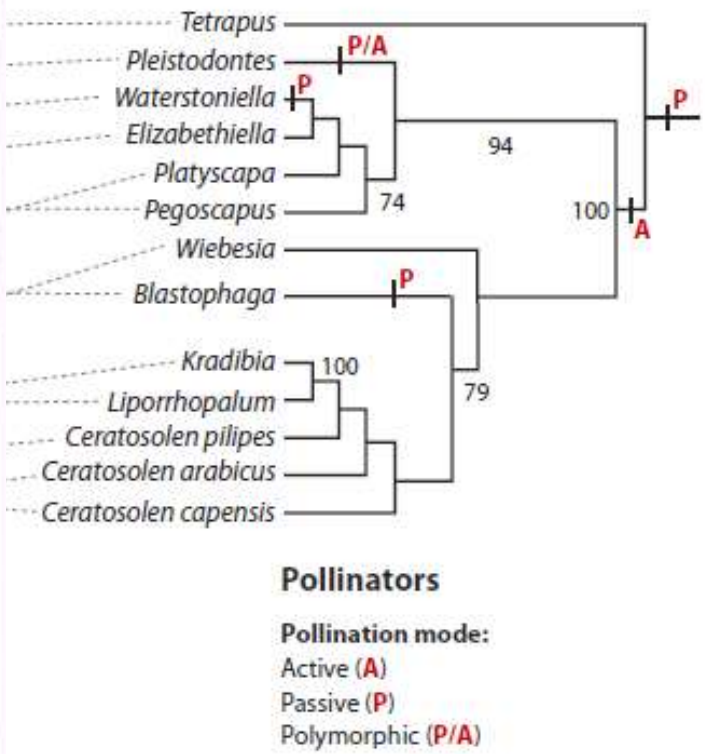
Photo G. Weiblen

Agaonind fig wasps:

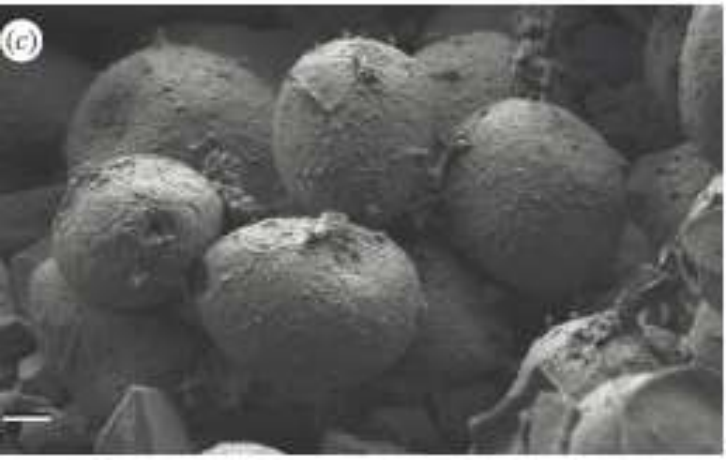
pollen pockets (pp) with pollen (po), coxal combs (cc) for brushing pollen







igure 1. Ventral views of female agaonid mesosoma from mainly actively pollinating genera: (*a*) *Pegoscapus hoffeyi* (host *Ficus lagunae*), (*b*) *Blastophaga* (*V.*) *cenfera* (host *Ficus grassularioides*), (*c*) *Pleistodontes imperialis* (host *Ficus obliqissima*), (*d*) *Pleistodontes idiceti* (host *Ficus craseifer*), (*e*) *Ceratosolen constrictus* (host *Ficus condrata*) and (*f*) *Ceratosolen galili* (host *Ficus sycomorus*). The head pointing right or upward. Species pollinating actively are shown in *a–c* and *e*. Species pollinating passively are shown in *d* and . Abbreviations: pp, pollen pocket; po, pollen seen through pollen-pocket opening; cc, coxal comb. Scale bar, 100 μm.



Molecular clock:
fig-fig wasp relationship is >65 M years old, from the Cretaceous

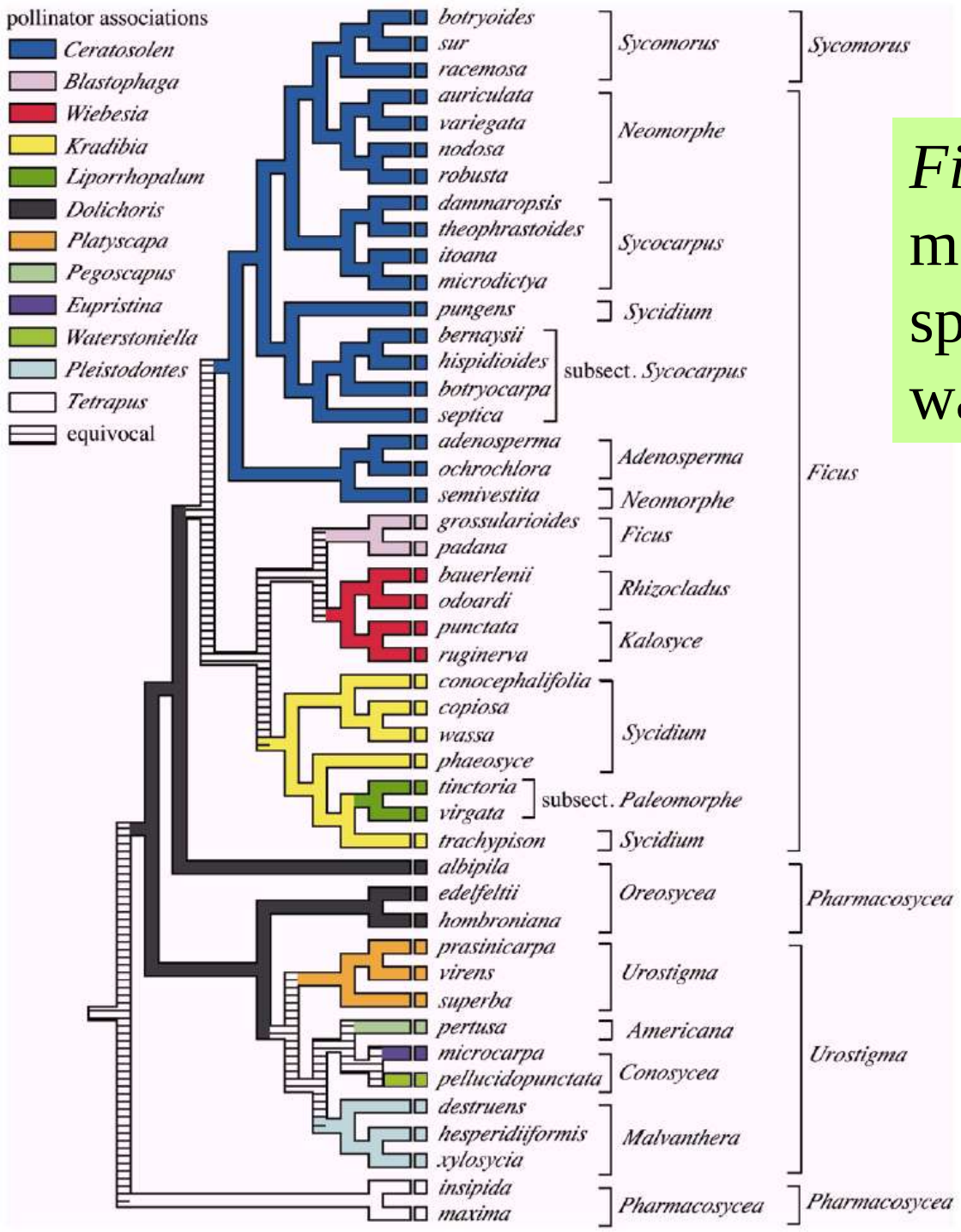
The oldest fossil fig wasps (England): 34 Mya. They possess pollen pockets with fossil Ficus pollen.

No innovations in the relationship are discernible for the last tens of millions of years.

Compton et al. Biol. Lett. (2010) 6, 838–842

Fig wasp emerging from a parasitised seed

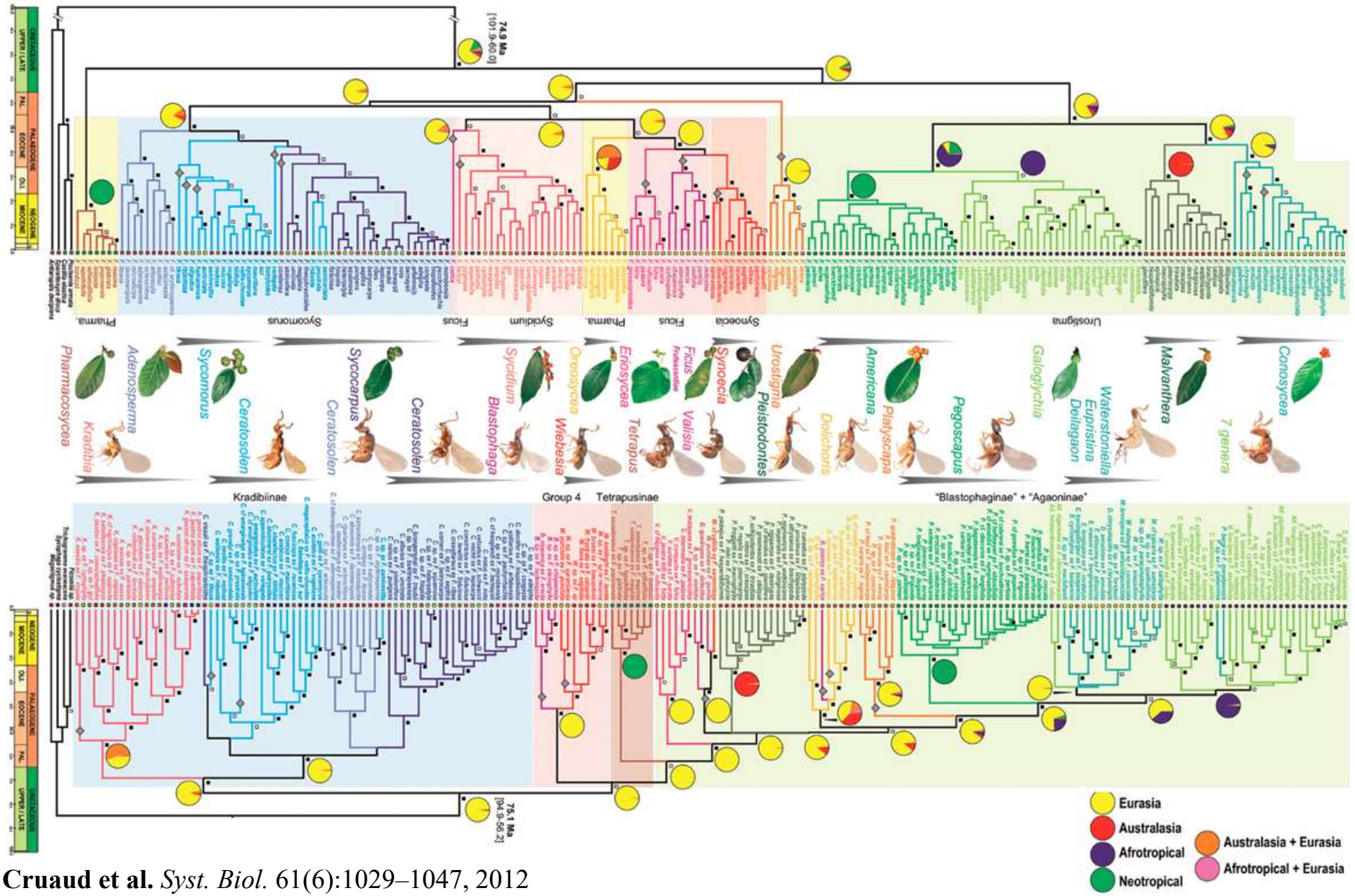
Photo G. Weiblen



Ficus phylogeny closely matches taxonomy of their specialised pollination wasps

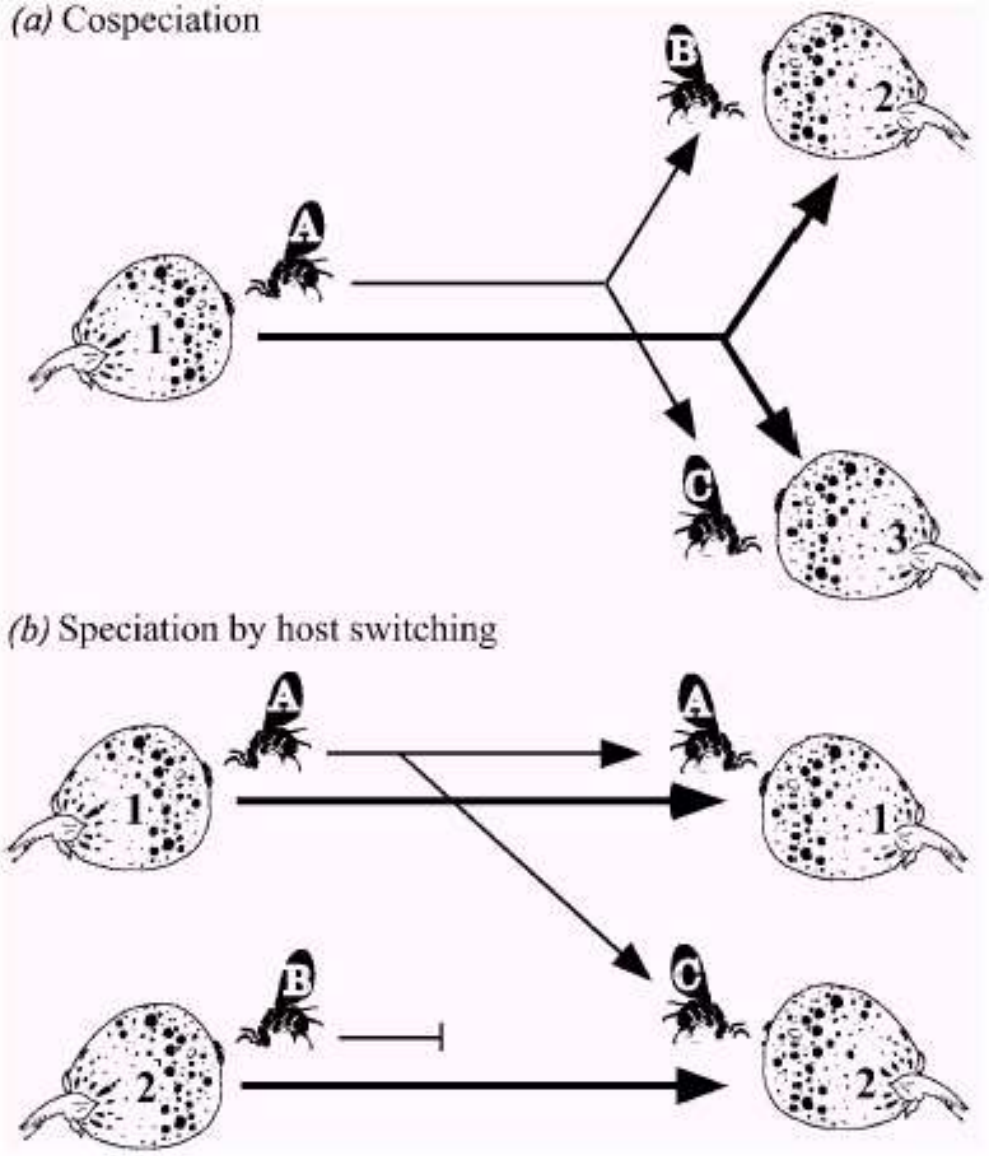
Weiblen 2004

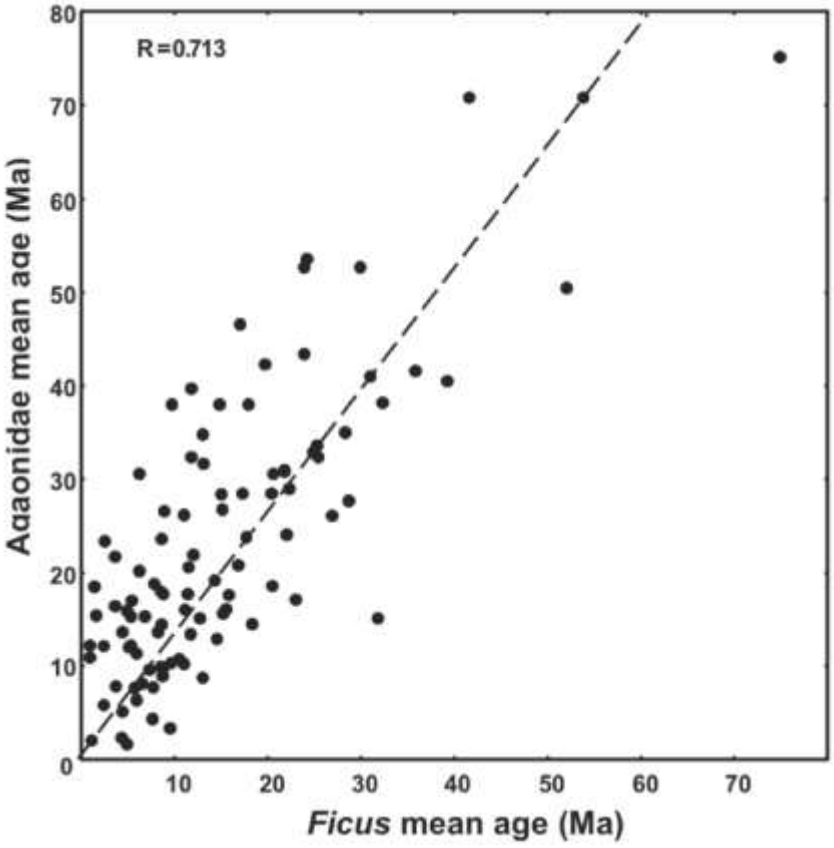
Ficus – pollinator wasp evolution



Cruaud et al. *Syst. Biol.* 61(6):1029–1047, 2012

How the fig - wasp relationships evolved?



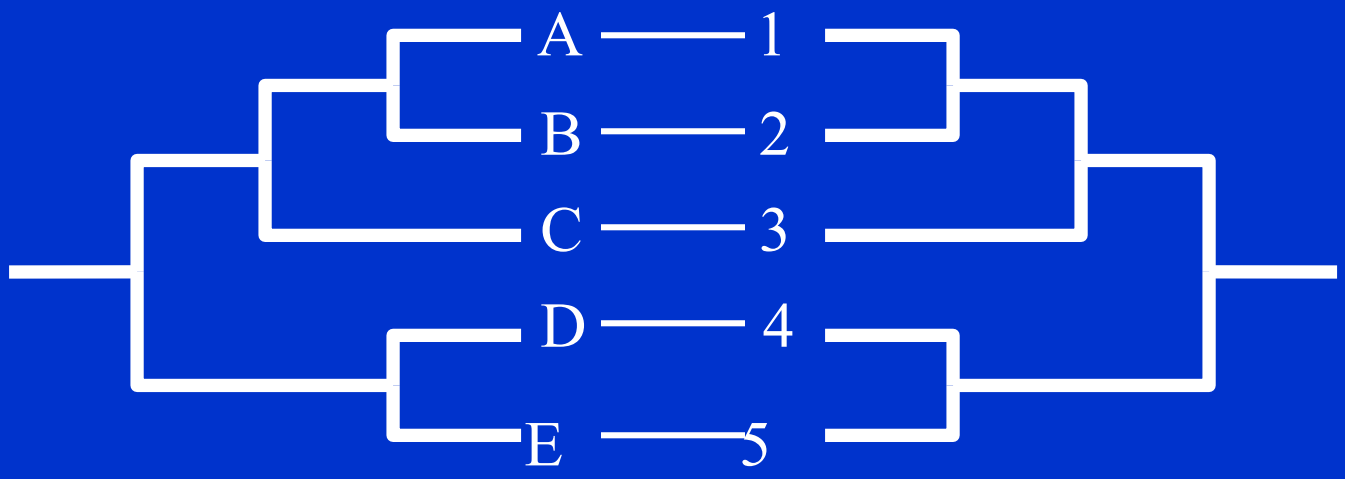


Temporal congruence of the 198 cospeciation events

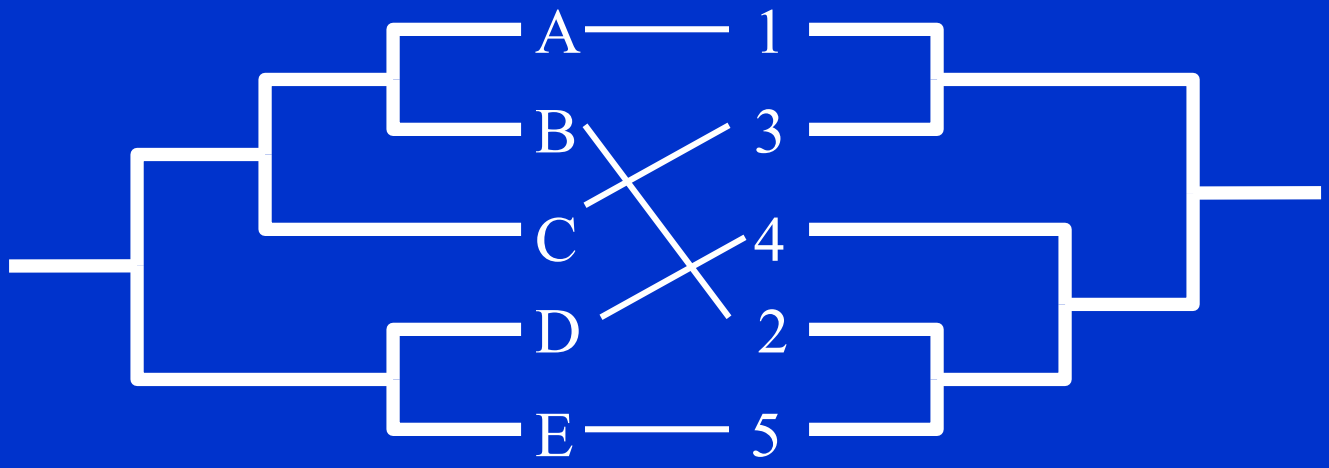
Weiblen 2002

Cruaud et al. *Syst. Biol.* 61(6):1029–1047, 2012

cospeciation

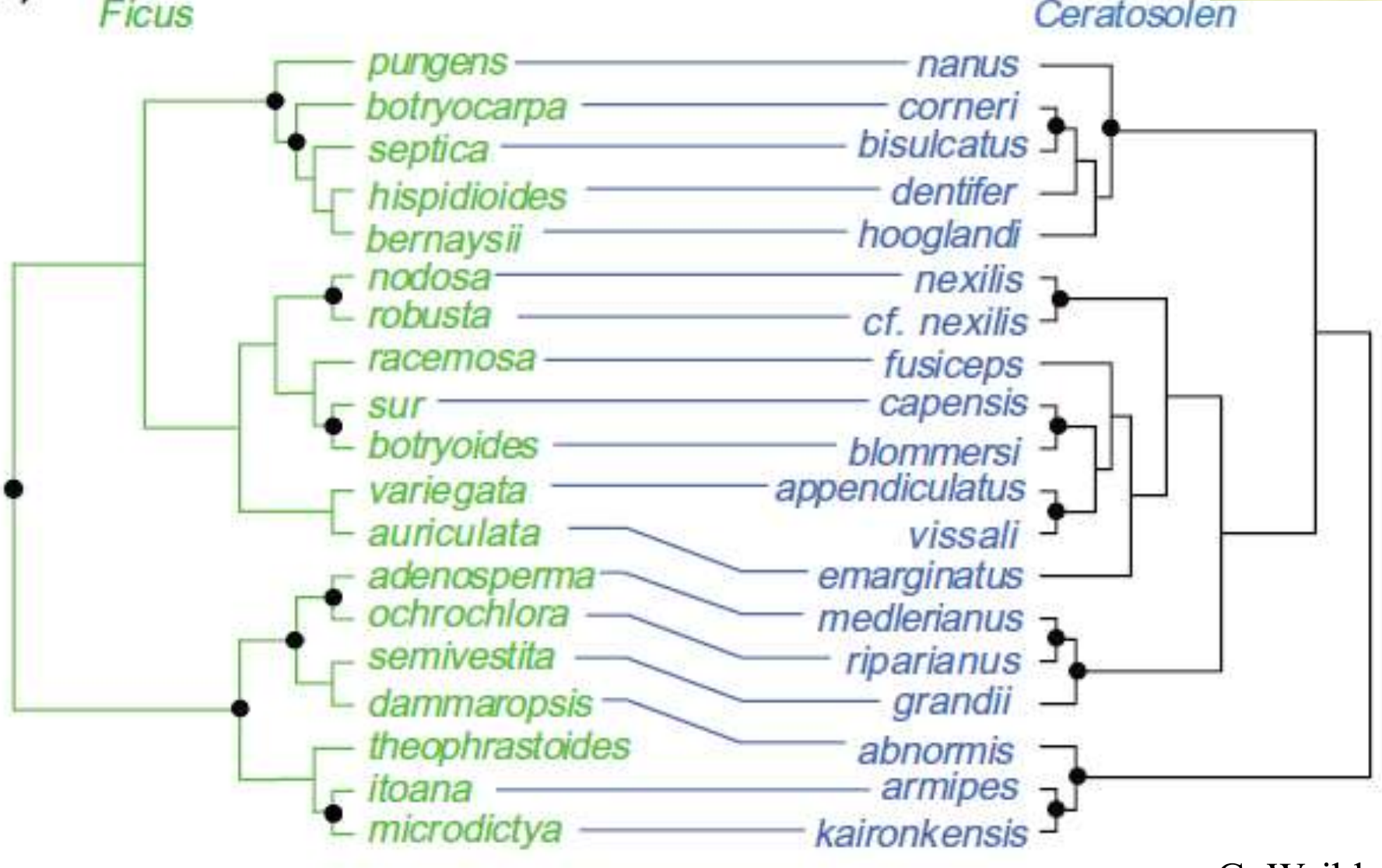


host switching



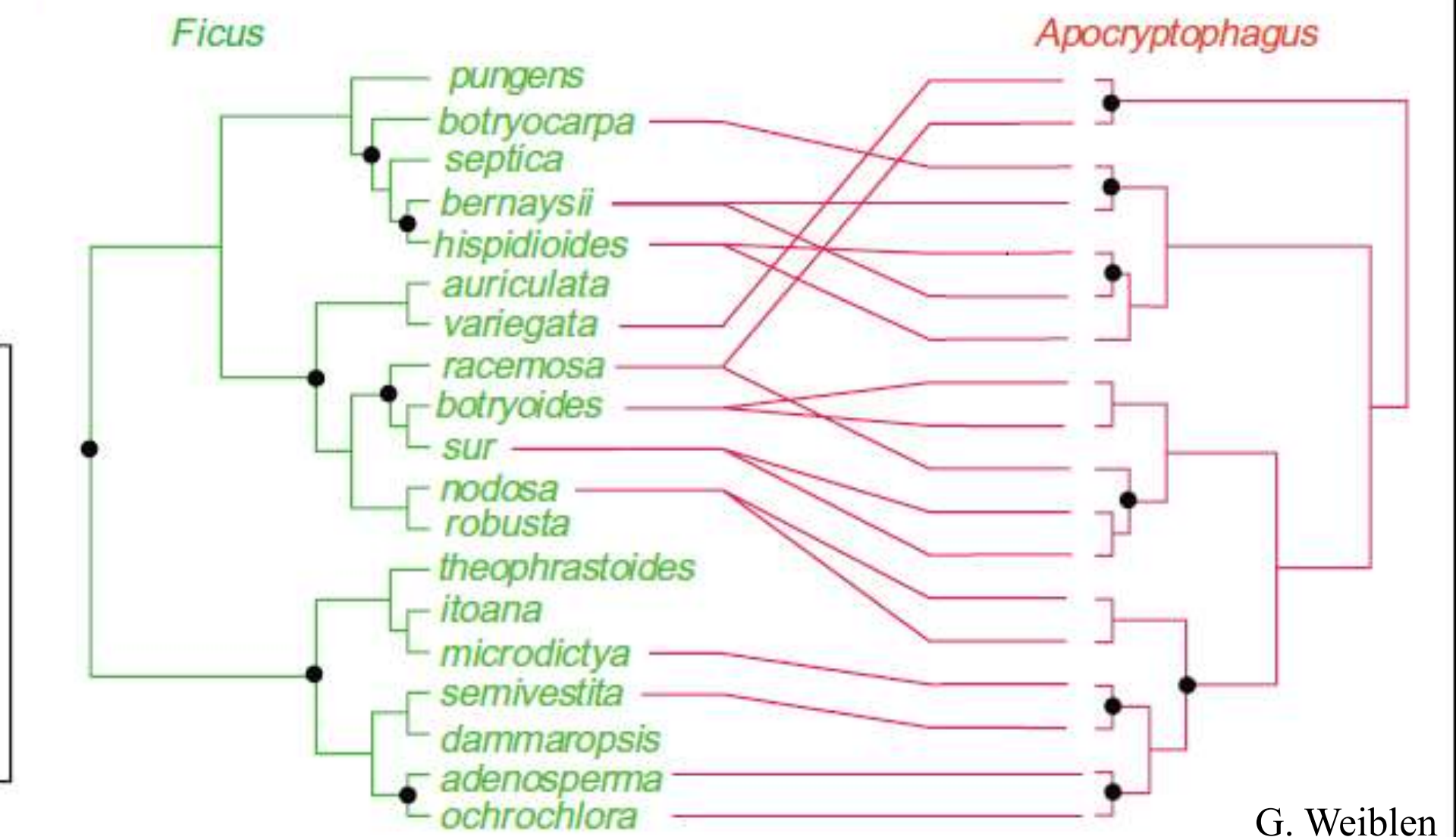
courtesy G. Weiblen

Ficus and their pollinating wasps



G. Weiblen

Ficus and non-pollinating galler wasps



G. Weiblen

Figs support also non-pollinating herbivorous wasps (gallers) and wasp parasitoids

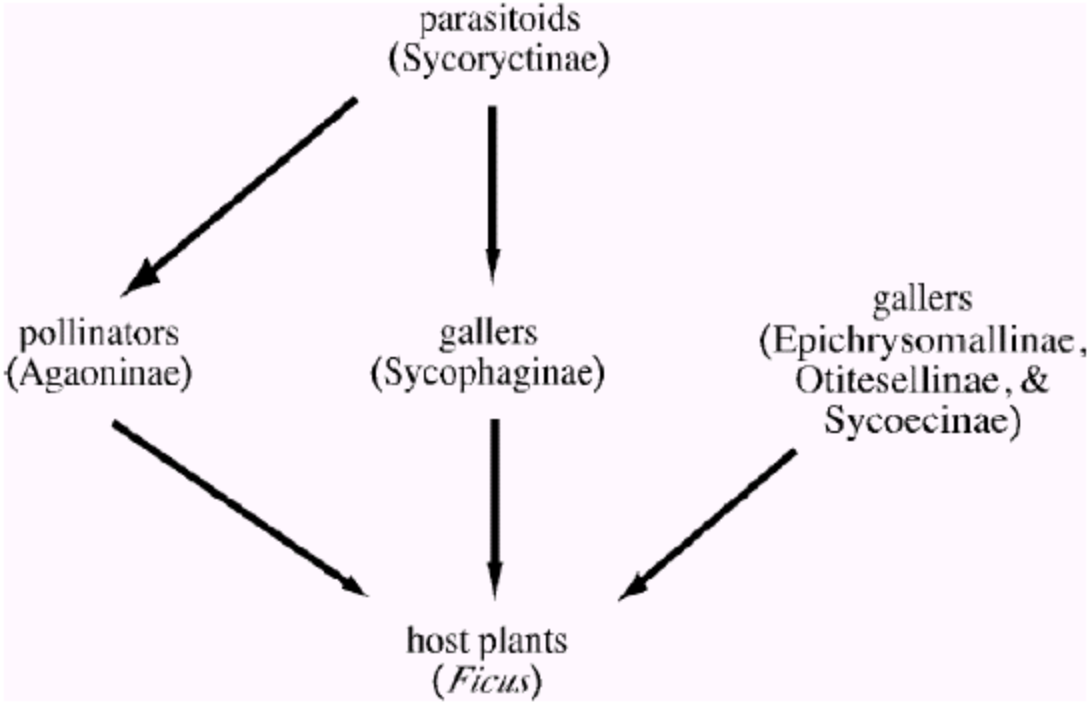
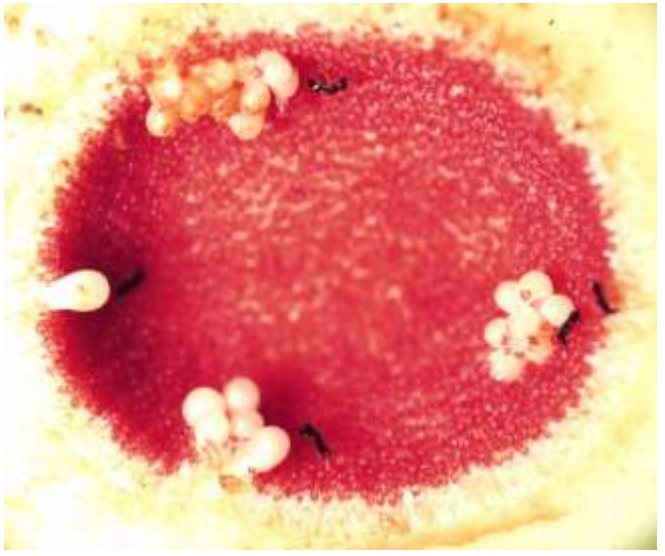
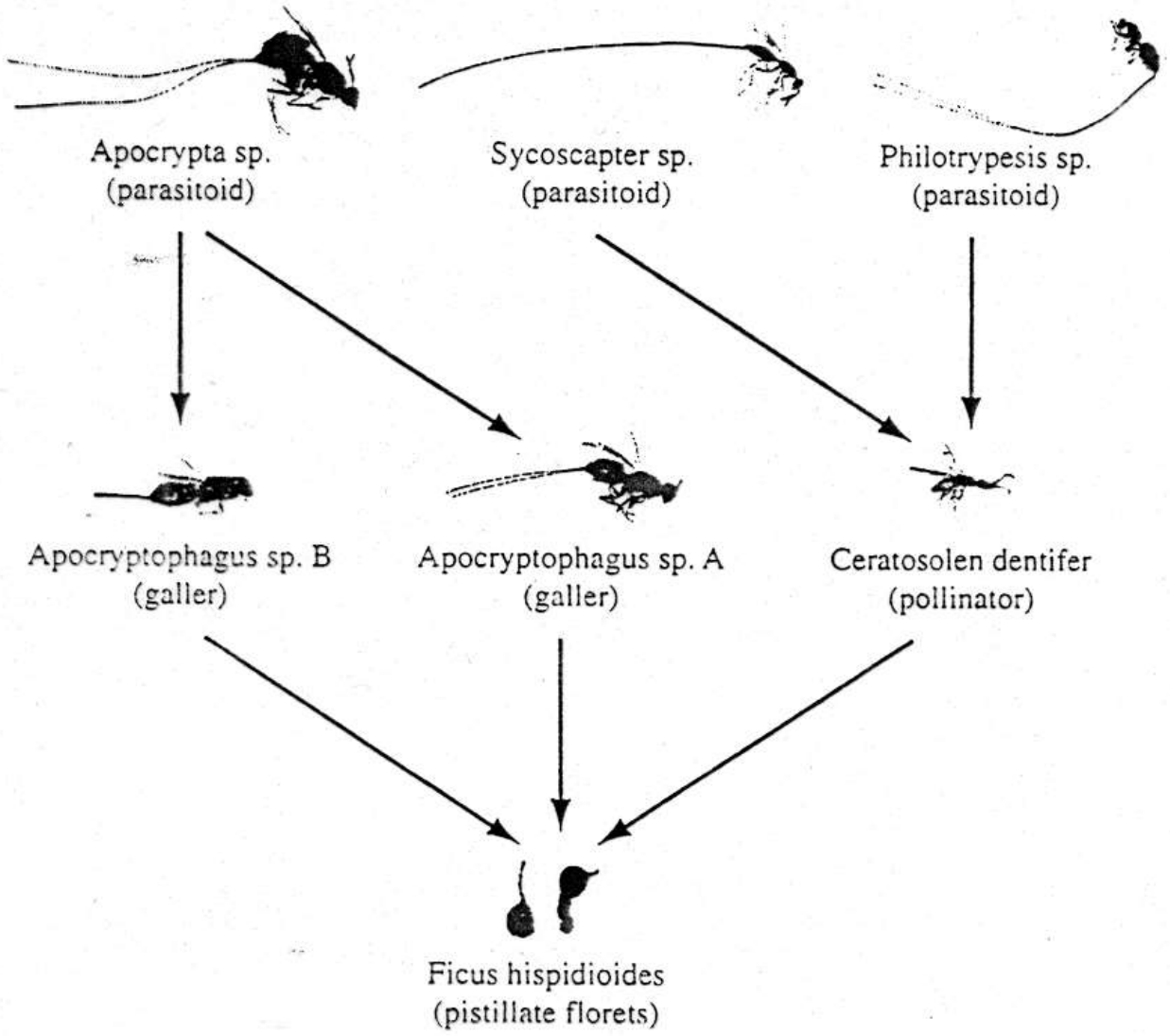


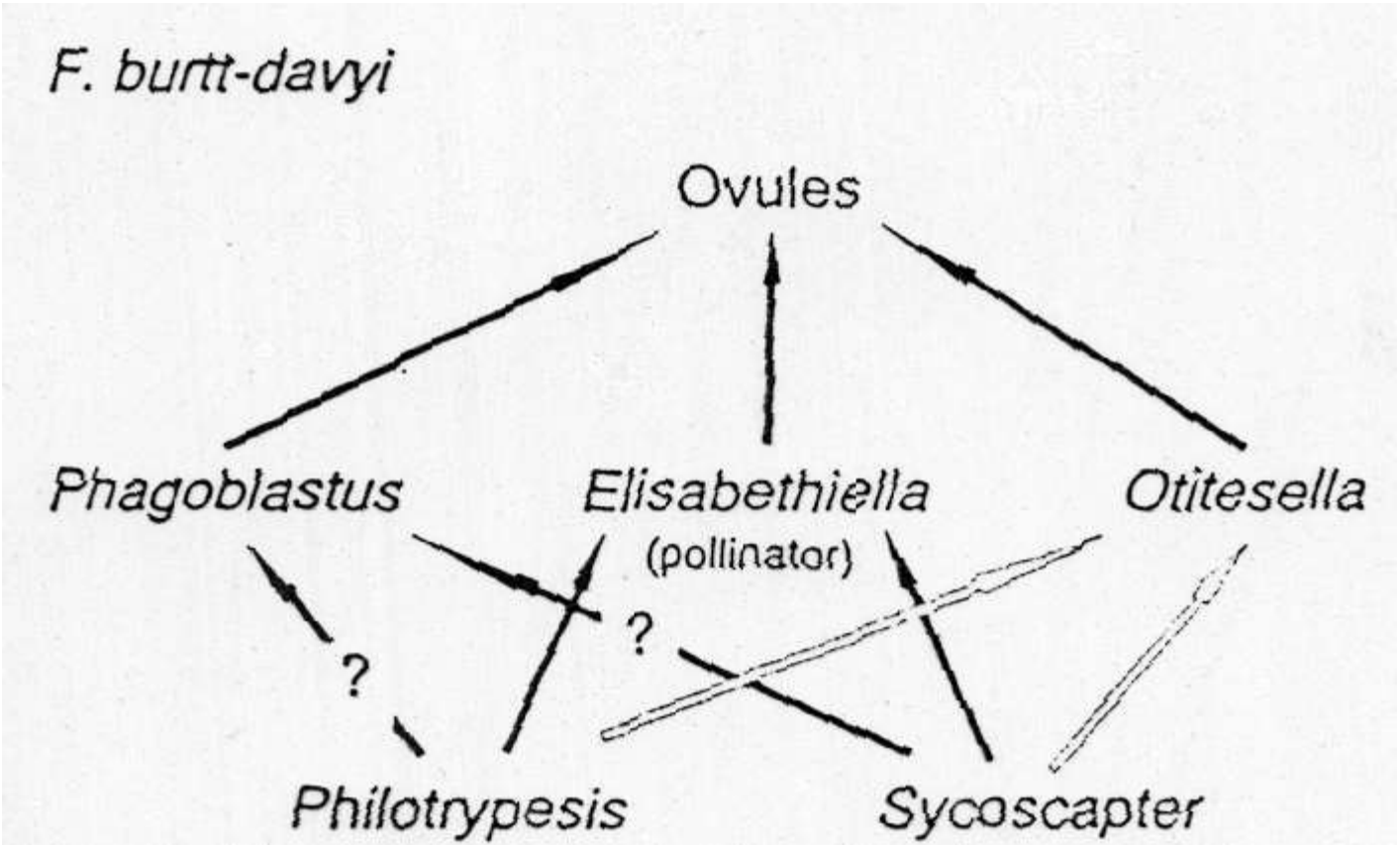
Figure 4 Trophic relationships among figs and fig wasps. Agaonid subfamilies include pollinators, gallers, and parasitoids.



Wasps on figs: pollinators, gallers and parasitoids



Weiblen et al. 2000



Food web of the fig wasps associated with *F. burtt-davyi* in the Grahamstown area of South Africa. Open arrows indicate uncommon interactions.

Apocryptophagus

Parasitic wasps

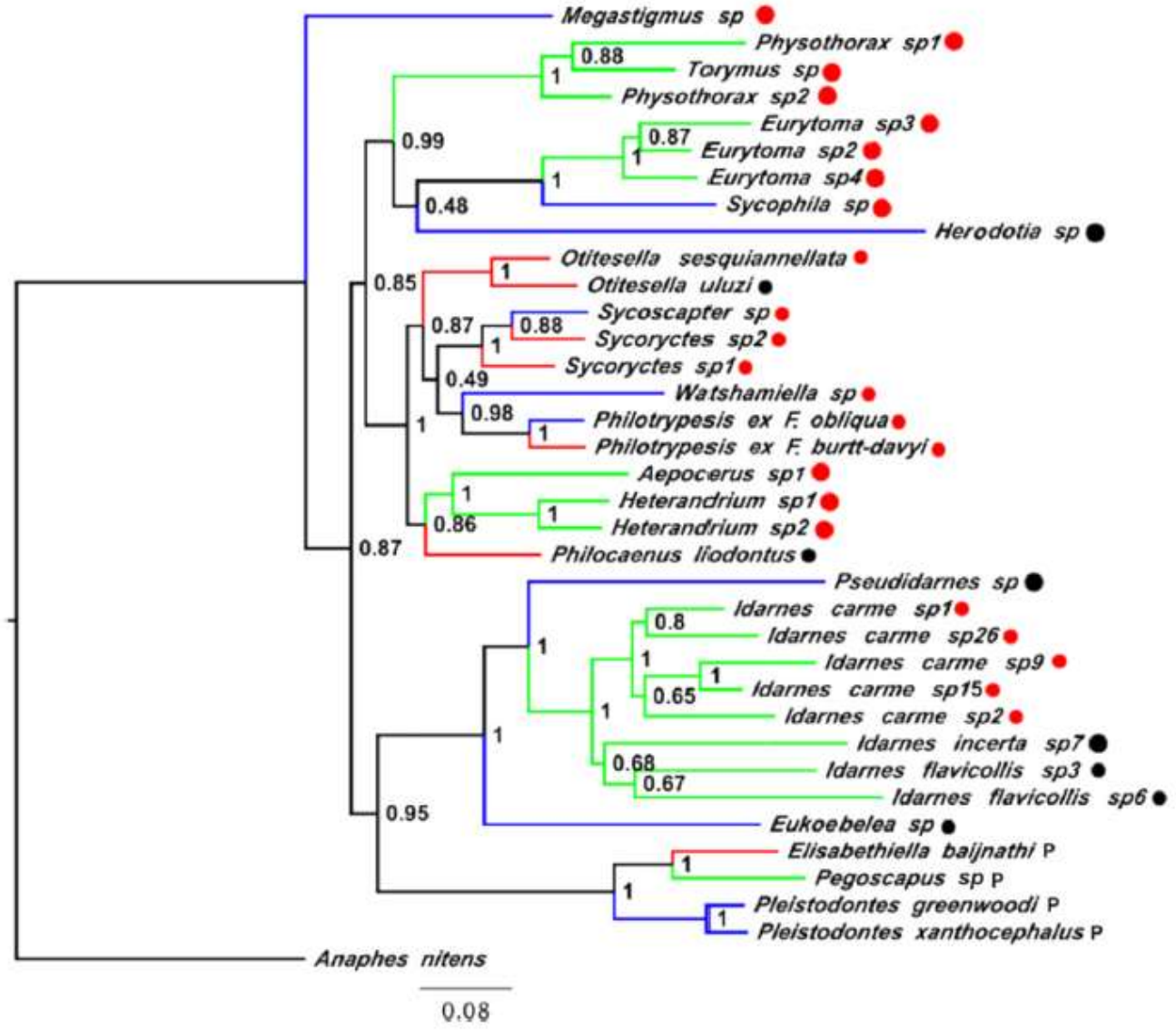
Photo G. Weiblen

All 35 wasp species from 3 Ficus spp.

F. obliqua

F. burtt-davyi

F. citrifolia

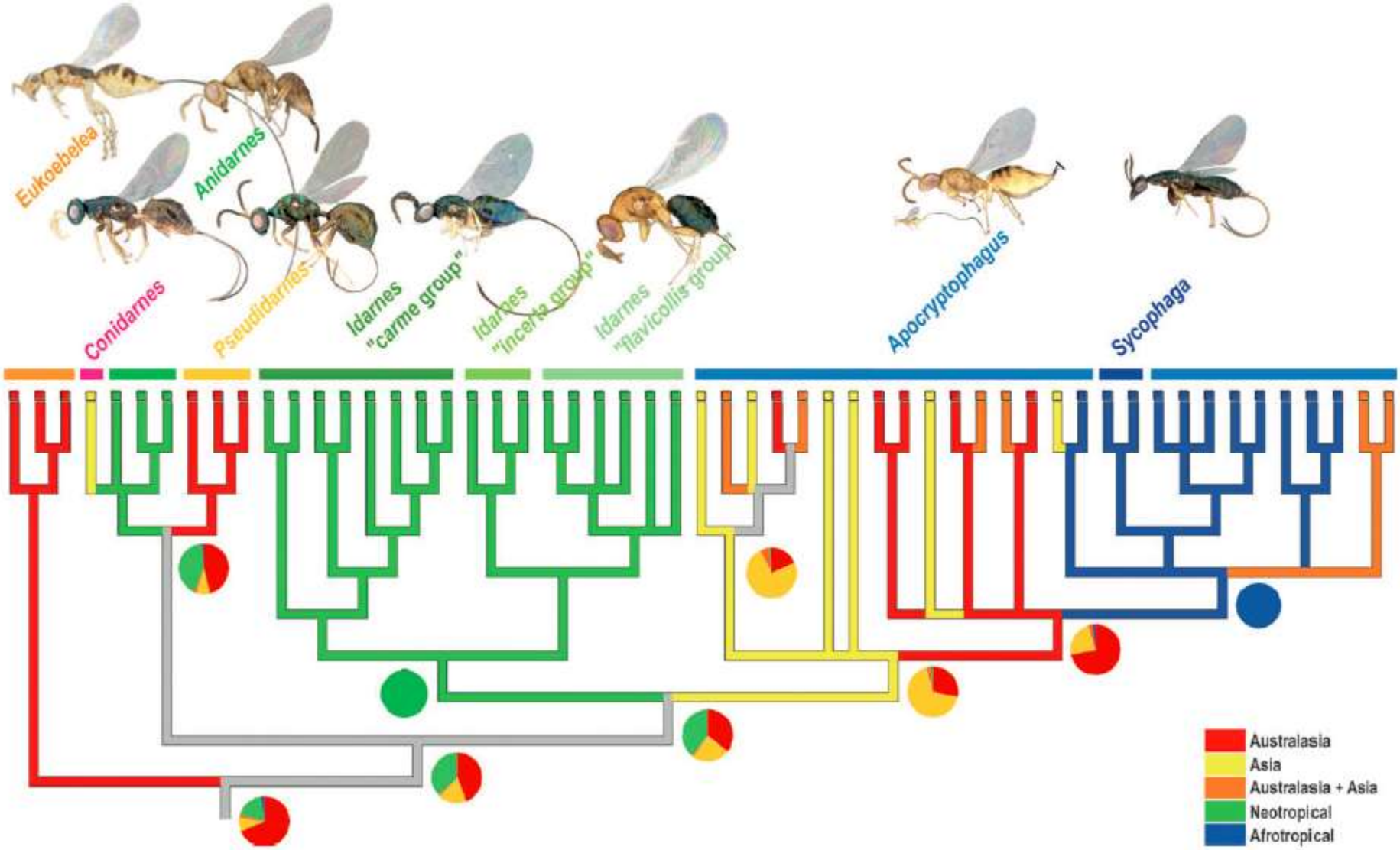


large parasitoids **large gallers**

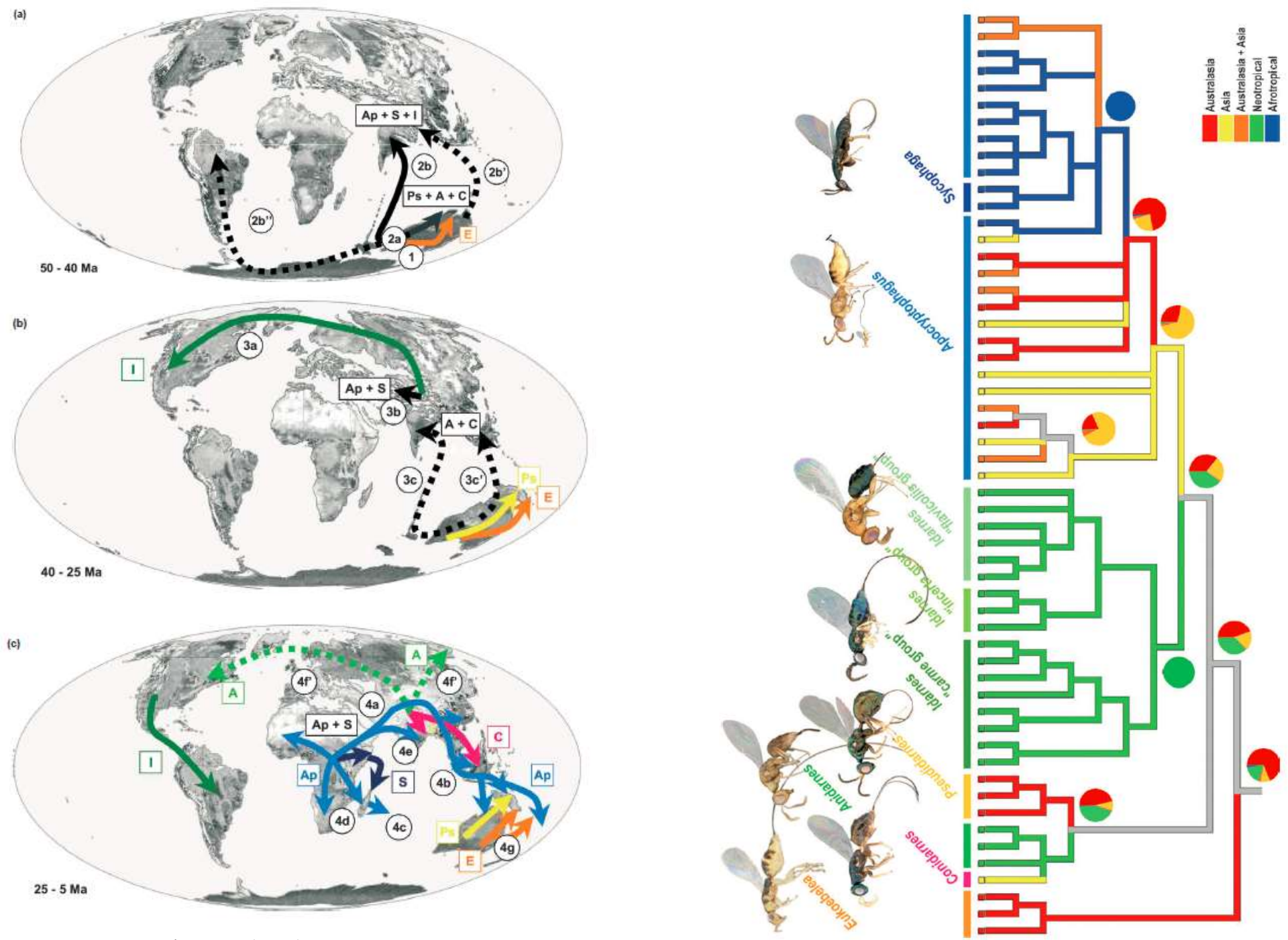
P pollinators **small parasitoids** **small gallers**

Segar et al. Ecology Letters, (2013) 16: 1436–1445

Galling Sycophaginae (Chalcidoidea, Hymenoptera) probably invaded the fig microcosm in Australia c. 50–40 Ma after the origin of their host plant, then dispersed out of Australia and radiated together with their host fig and associated pollinator through the tropics.



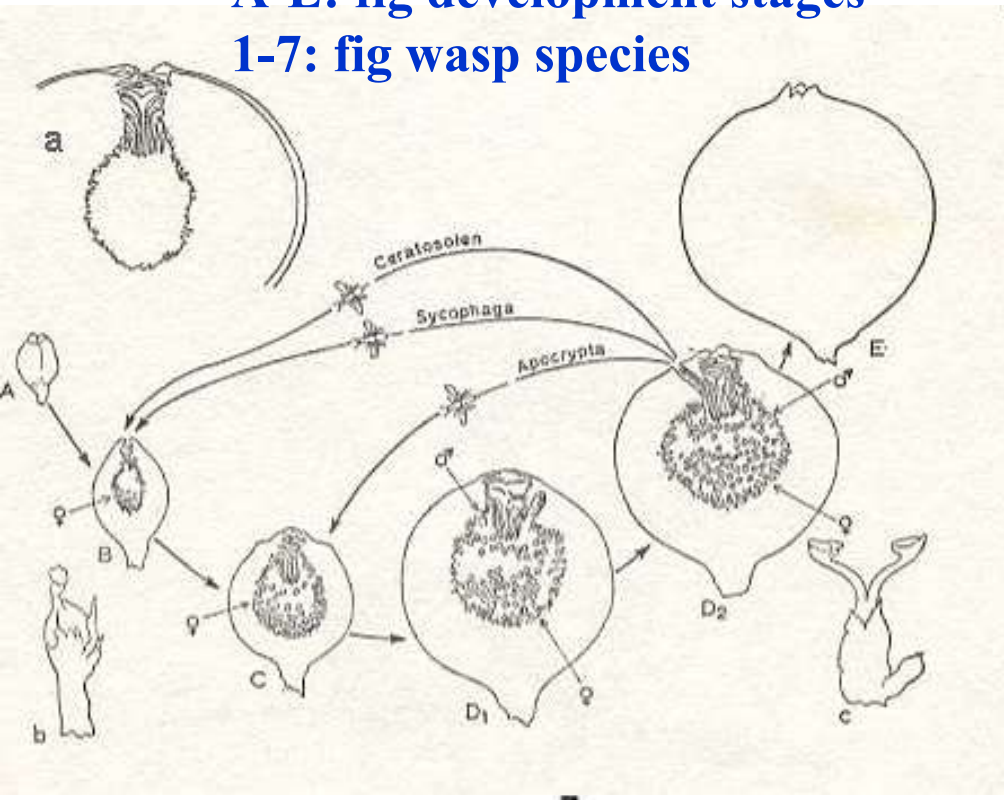
Cruaud et al. J. Biogeogr. (2011) 38, 209–225

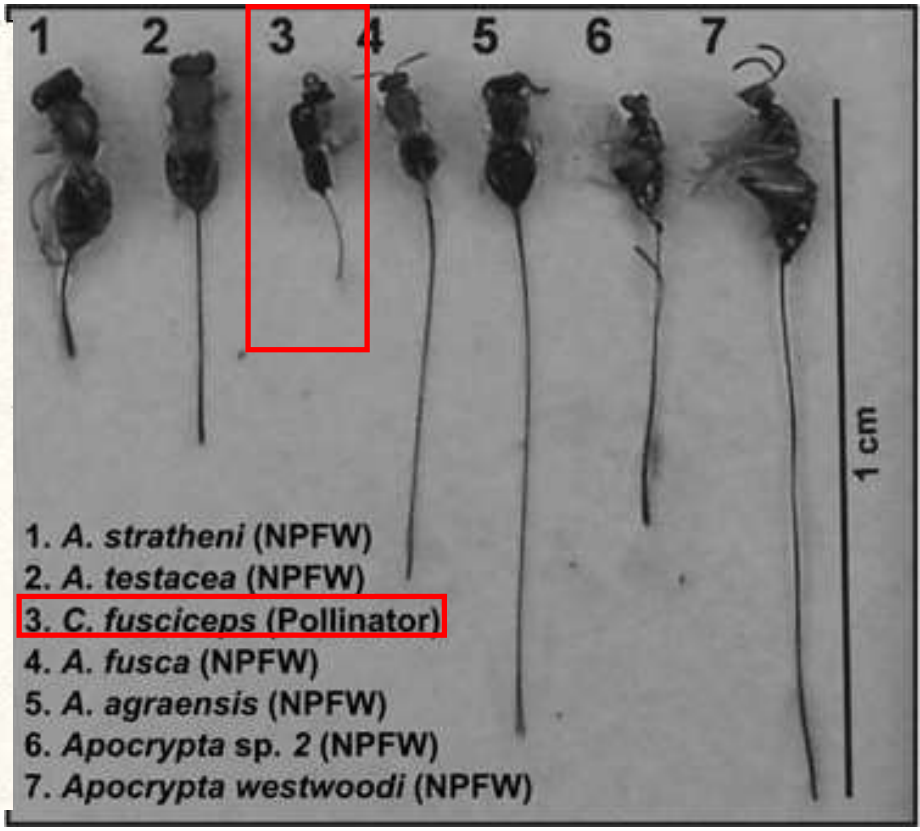


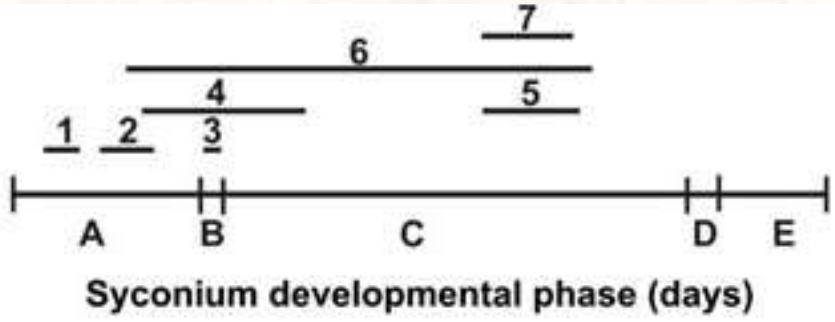
Cruaud et al. J. Biogeogr. (2011) 38, 209–225

Oviposition succession of 1 pollinating and 6 non-pollinating wasp species during fig development depends on ovipositor length [and vice versa, ovipositor length is selected for by fig size]

A-E: fig development stages
1-7: fig wasp species



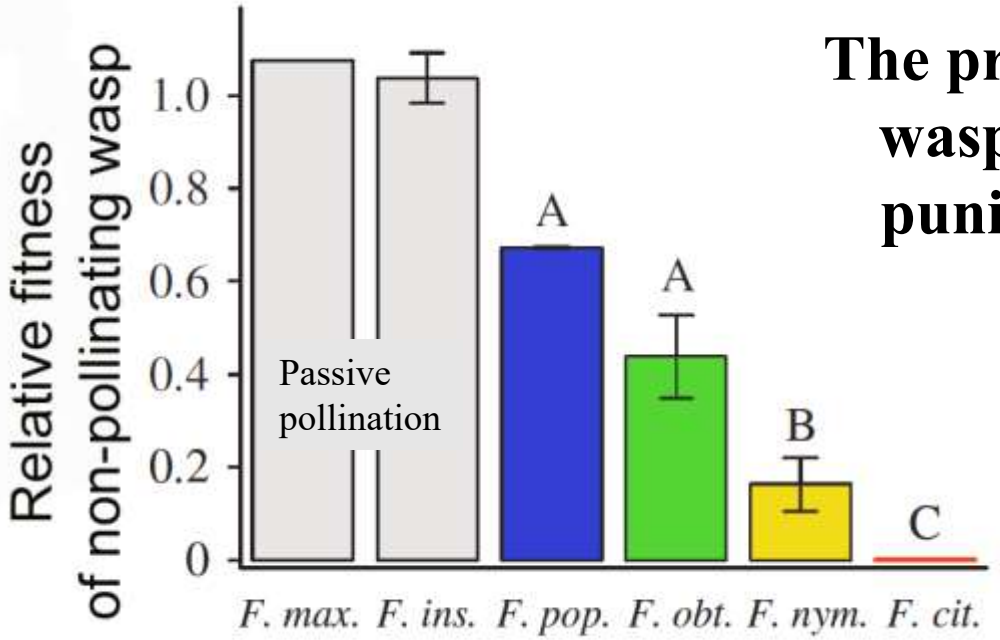


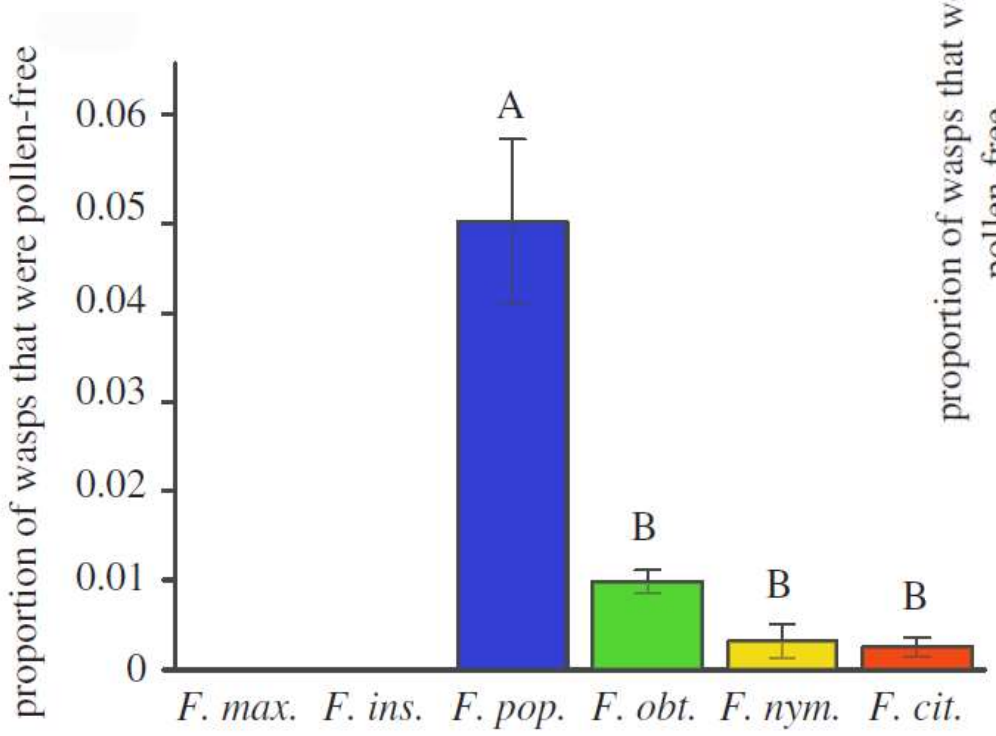


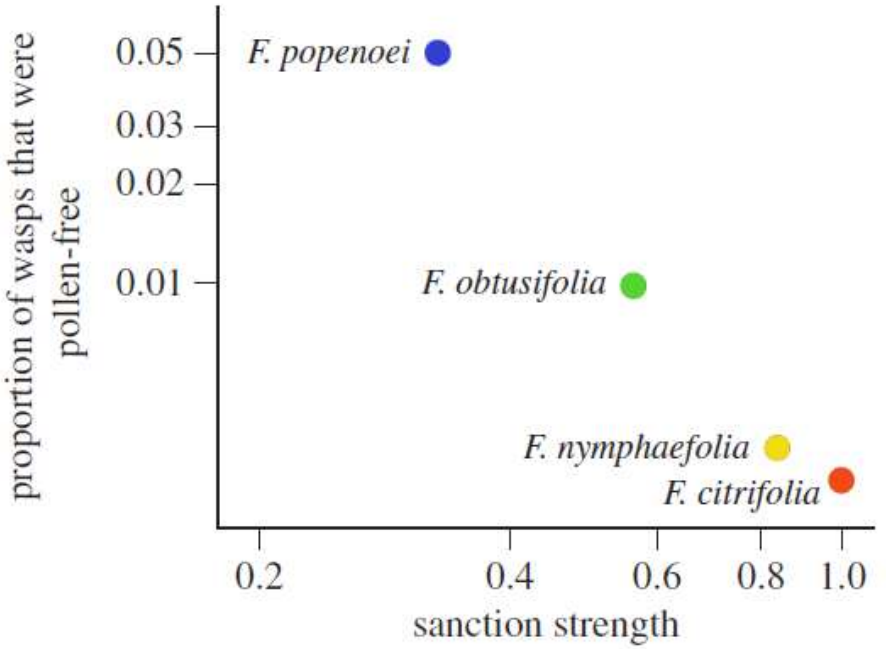
Ficus racemosa

Ghara & Borges (2010) Ecol. Ent. 35: 139-148.

The proportion of non-pollinating fig wasps depends on the strength of punishment for cheating by their host fig species

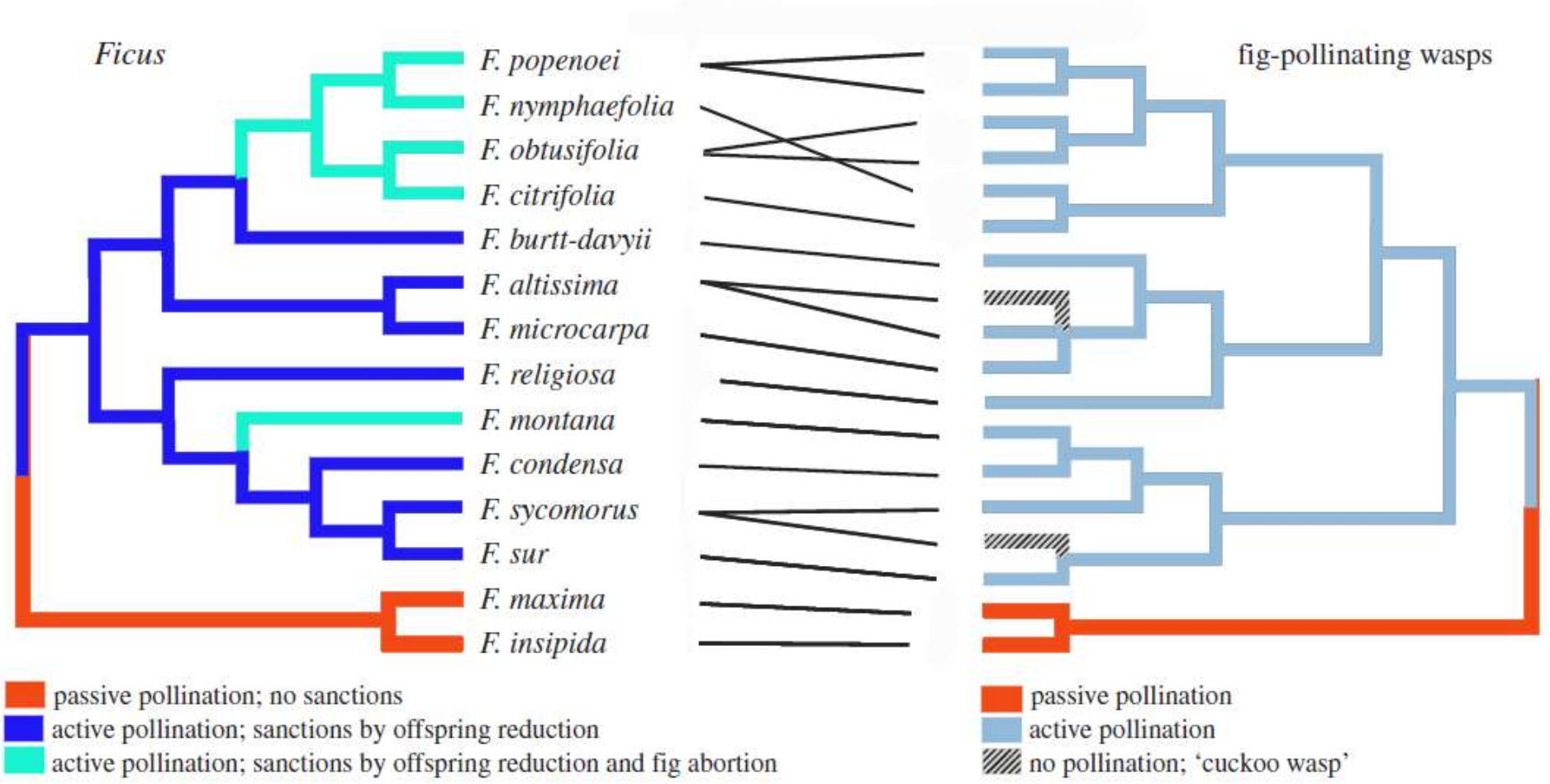






Jander & Herre 2010, Proc. R. Soc. B **277**, 1481-1488

Sanction for no pollination: offspring reduction and fig abortion



passive pollination – no energy expenditure, no pollen-free wasps, no sanctions

active pollination – demands energy, cheaters sanctioned by figs

Jander & Herre 2010, Proc. R. Soc. B **277**, 1481-1488

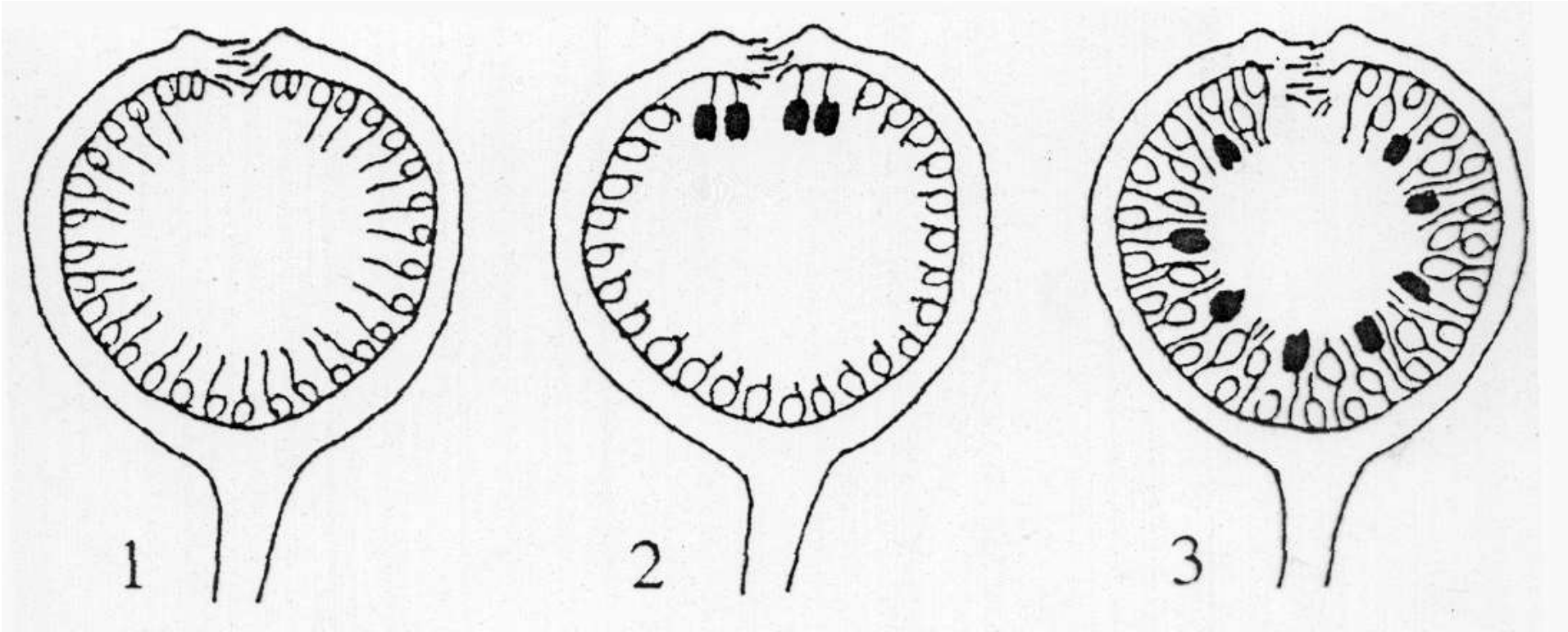
Gynodioecious species

Monoecious species

seed production

pollen & wasp production

seed, pollen & wasp production



Figs. 1–3. The distribution of unisexual florets in figs (syconia) of monoecious and gynodioecious *Ficus*. There are two types of figs on separate plants in gynodioecious *Ficus*, seed figs containing long-styled pistillate florets (Fig. 1) and gall figs containing short-styled pistillate florets and staminate florets (Fig. 2). Monoecious species have a single type of fig containing pistillate florets with styles of varying length and staminate florets (Fig. 3). Anthers are blackened to indicate the position of staminate florets near the ostiole in Fig. 2 and dispersed among the pistillate florets in Fig. 3.

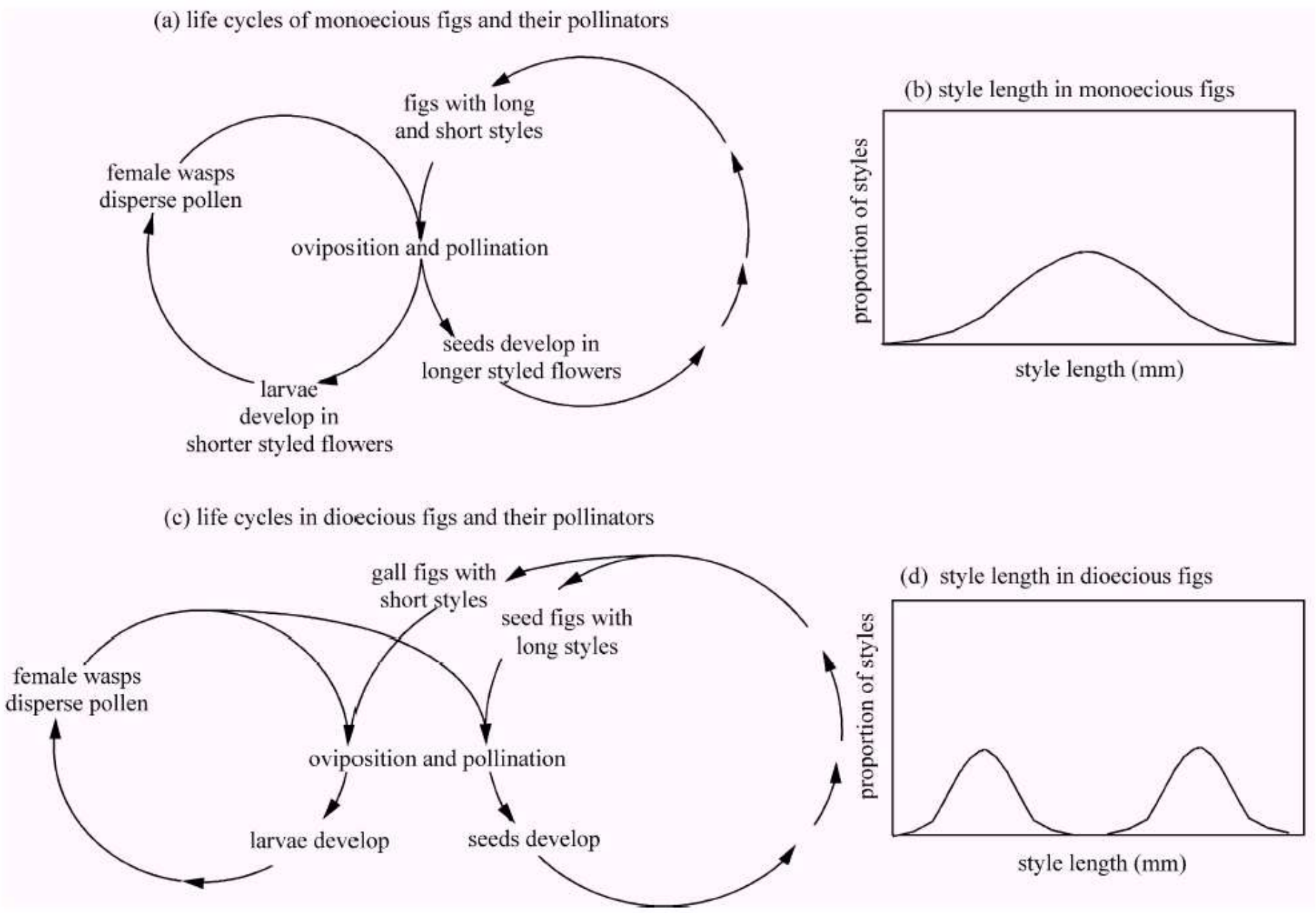
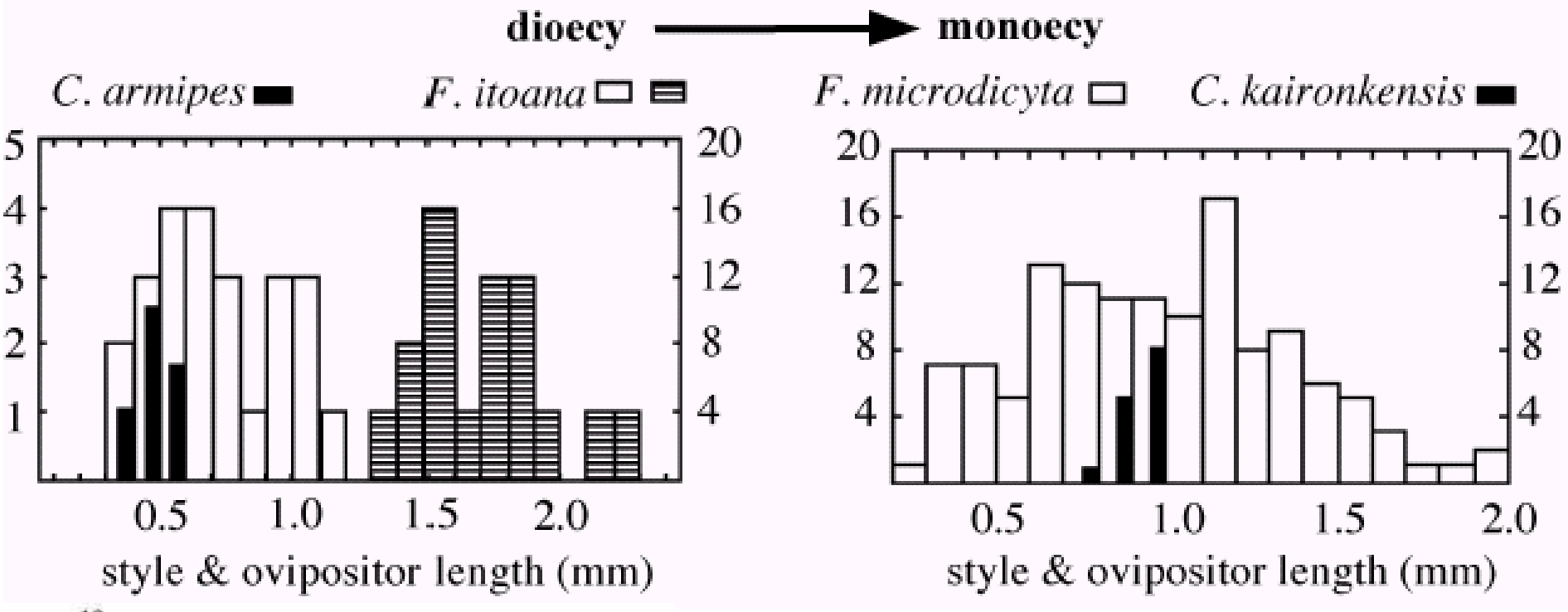
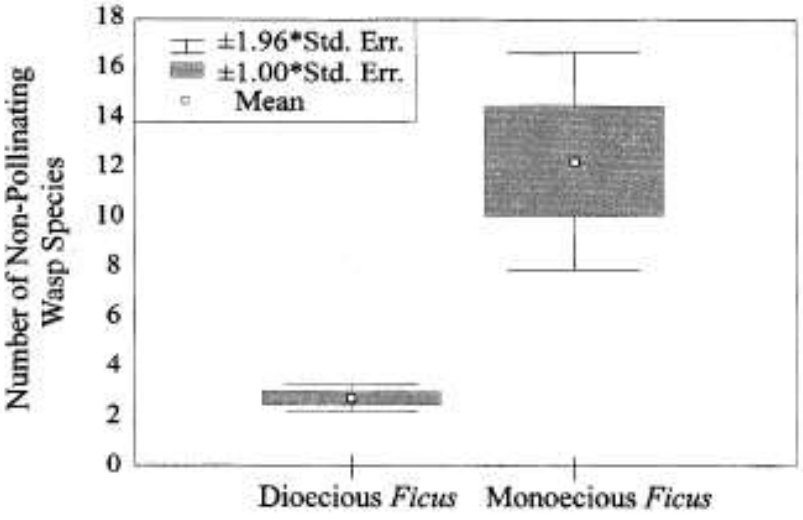


FIGURE 1. Life cycles of monoecious and functionally dioecious *Ficus* and their pollinators. (a) In monoecious species, seeds and pollinators develop in the same fig. (b) The distribution of style lengths in monoecious figs is unimodal, but pollinators tend to develop in shorter styled flowers and seeds tend to develop in longer styled flowers. (c) In functionally dioecious species, the production of pollinators and seeds is segregated in two types of figs on separate plants. (d) Style length dimorphism divides the maturation of pollinators and seeds into gall figs (first mode) and seed figs (second mode), respectively.

Weiblen 2004

Style and ovipositior lengths in monoecious and dioecious figs





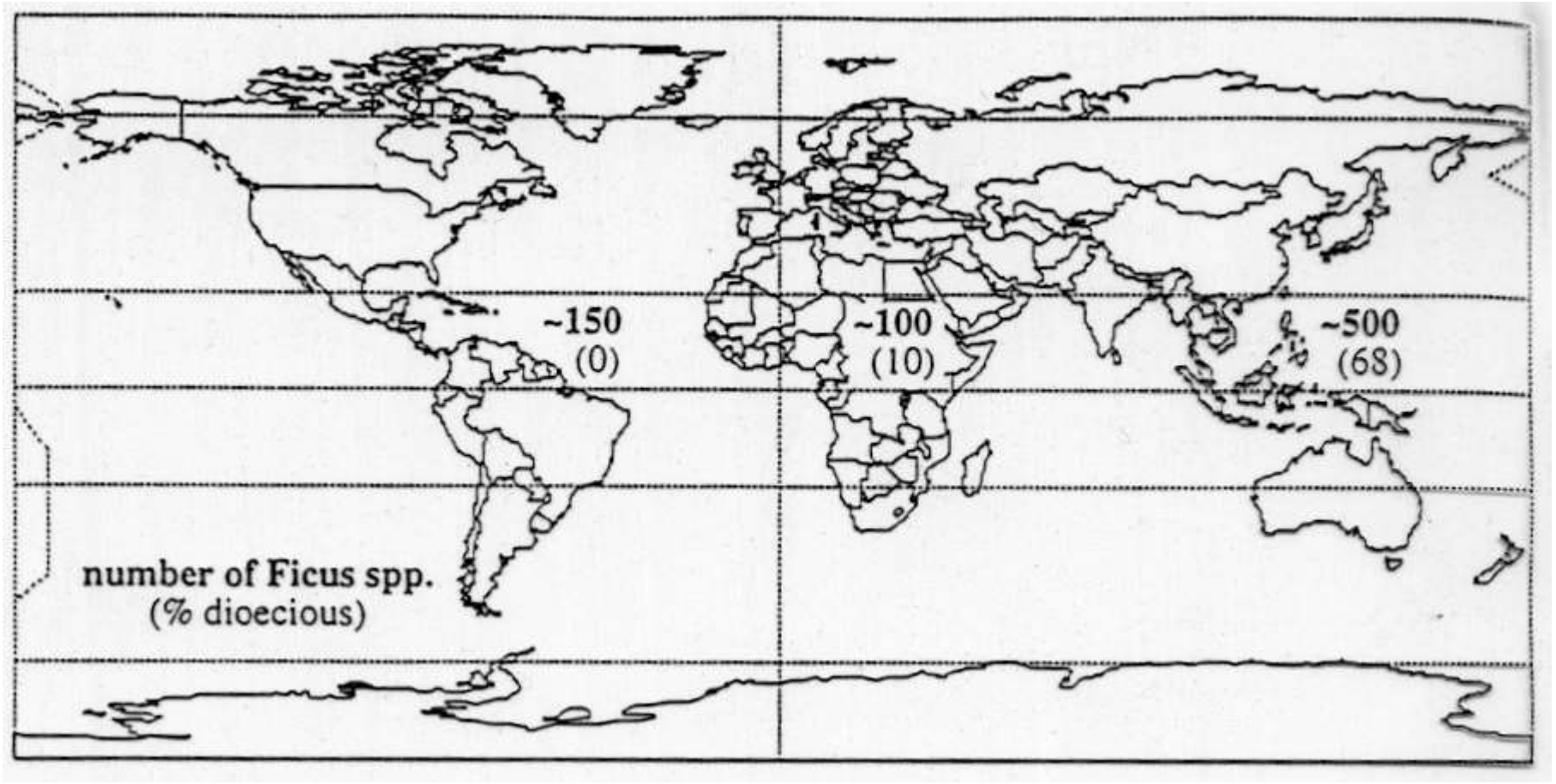
Why gynodioecy?
perhaps to reduce the number of non-pollinating wasps

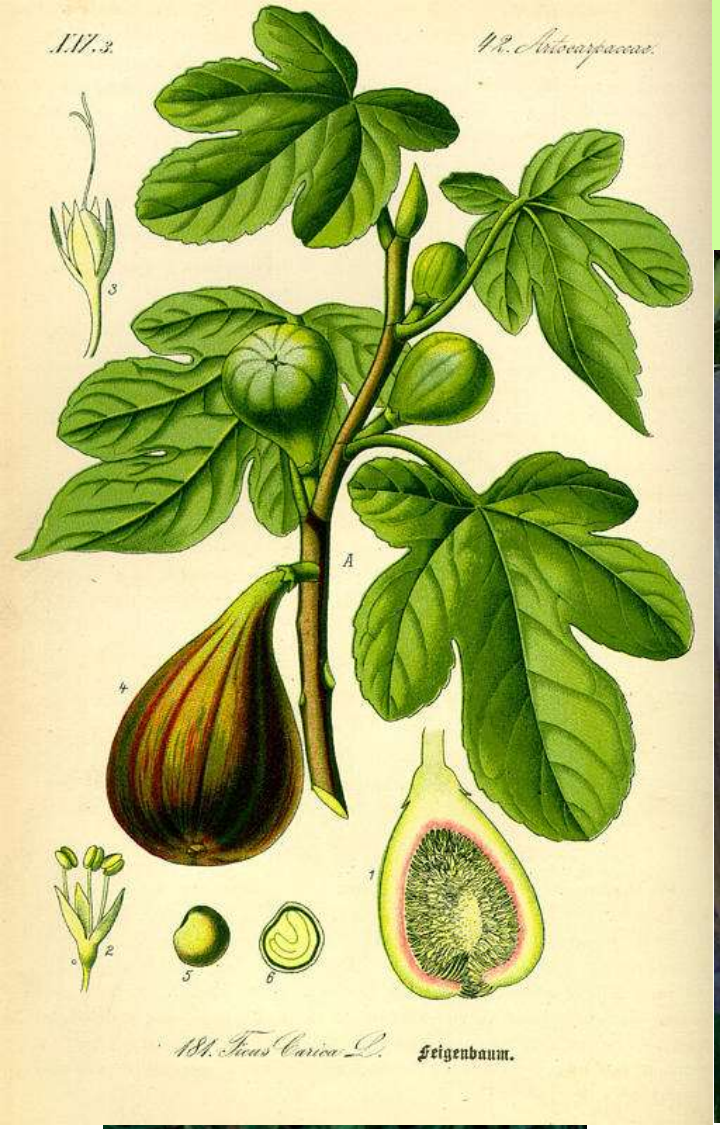
Kerdelhue & Rasplus OIKOS 77:1 (1996)

Weiblen 2004

of dioecious *Ficus itoana* and monoecious *F. microdictya* and their pollinators, an unambiguous cospe-
. Frequency distributions of style lengths (open and hatched bars) and ovipositor lengths (solid bars)
to monoecy in a dioecious clade (Weiblen, 2000). Hatched bars represent style lengths in seed figs. The
es are scaled at the left and right of each plot, respectively.

Gynodioecious figs evolved only in the Palaeotropics

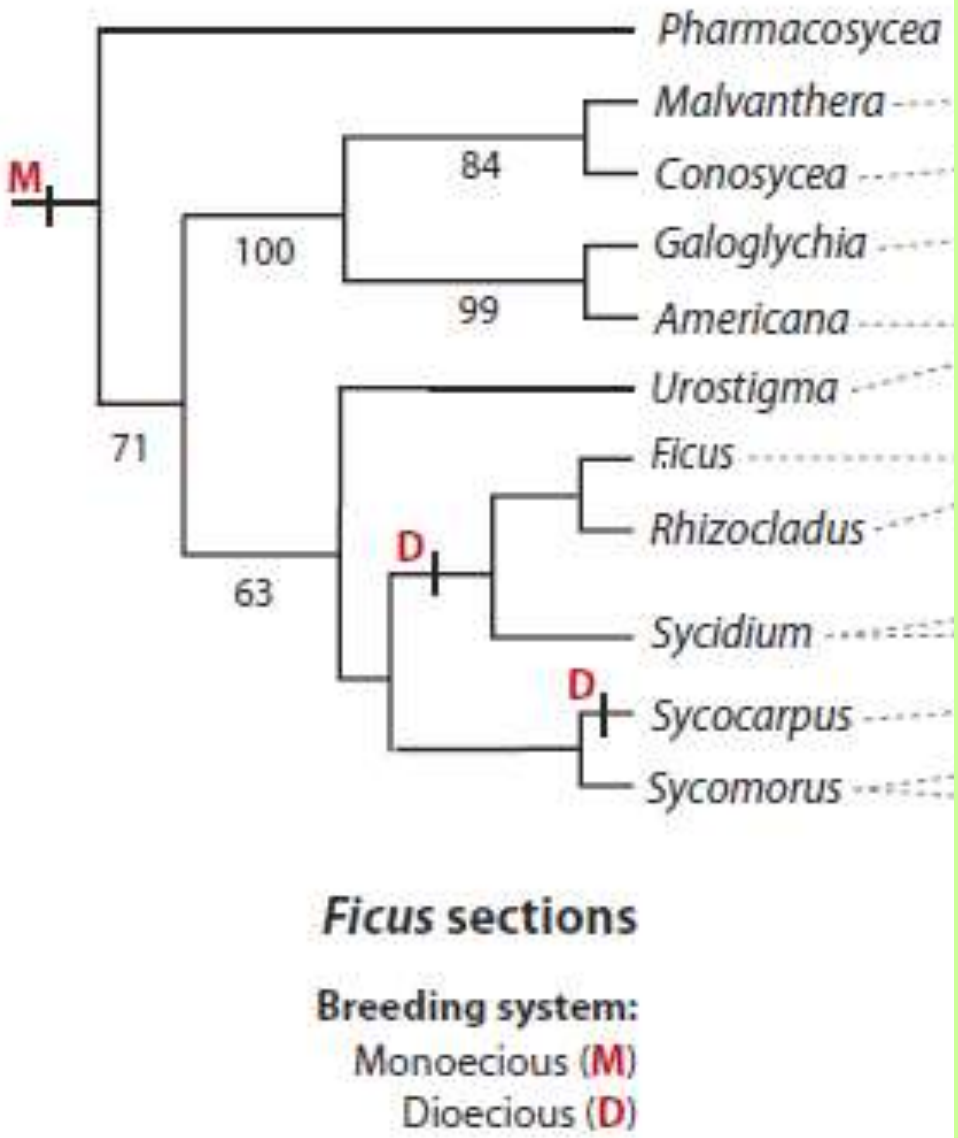




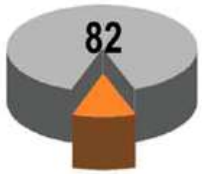
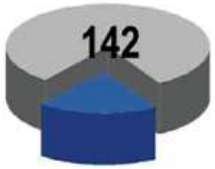
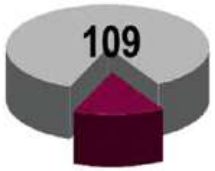
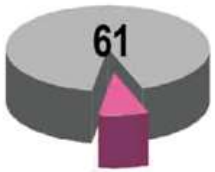
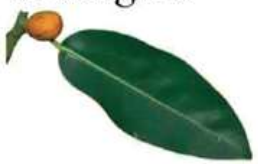
Ficus carica:
the most famous gynodioecious fig

Whoso keepeth the fig tree shall eat the fruit thereof: so he that waiteth on his master shall be honoured. Proverbs 27:18

two origins of dioecy



Herre et al. Annu. Rev. Ecol. Evol. Syst. 2008. 39:439–58

Subgenera	Diversity	Section	Oecy	Distribution	Pollinator	Mode
Pharmacosycea 		*Pharmacosycea*	M		*Tetrapus*	P
		Oreosycea	M		*Dolichoris*	A
Sycomorus 		*Sycocarpus*	D		*Ceratosolen*	A
		Sycomorus	MD			
		Adenosperma	D			
Sycidium 		*Sycidium*	D		*Kradibia*	A
		Palaeomorphe	D			
Synoecia 		*Kissosycea*	D		*Wiebesia*	AP
		Rhizocladus	D			
Ficus 		*Ficus*	D		*Blastophaga*	P
		Eriosycea	D		*Valisia*	A
Urostigma 		*Americana*	M		*Pegoscapus*	AP
		Galoglychia	M		7 genera*	A
		Malvanthera	M		*Pleistodontes*	AP
		Urostigma	M		*Platyscapa*	AP
		Conosycea	M		*Eupristina* &	AP
					2 genera**	P

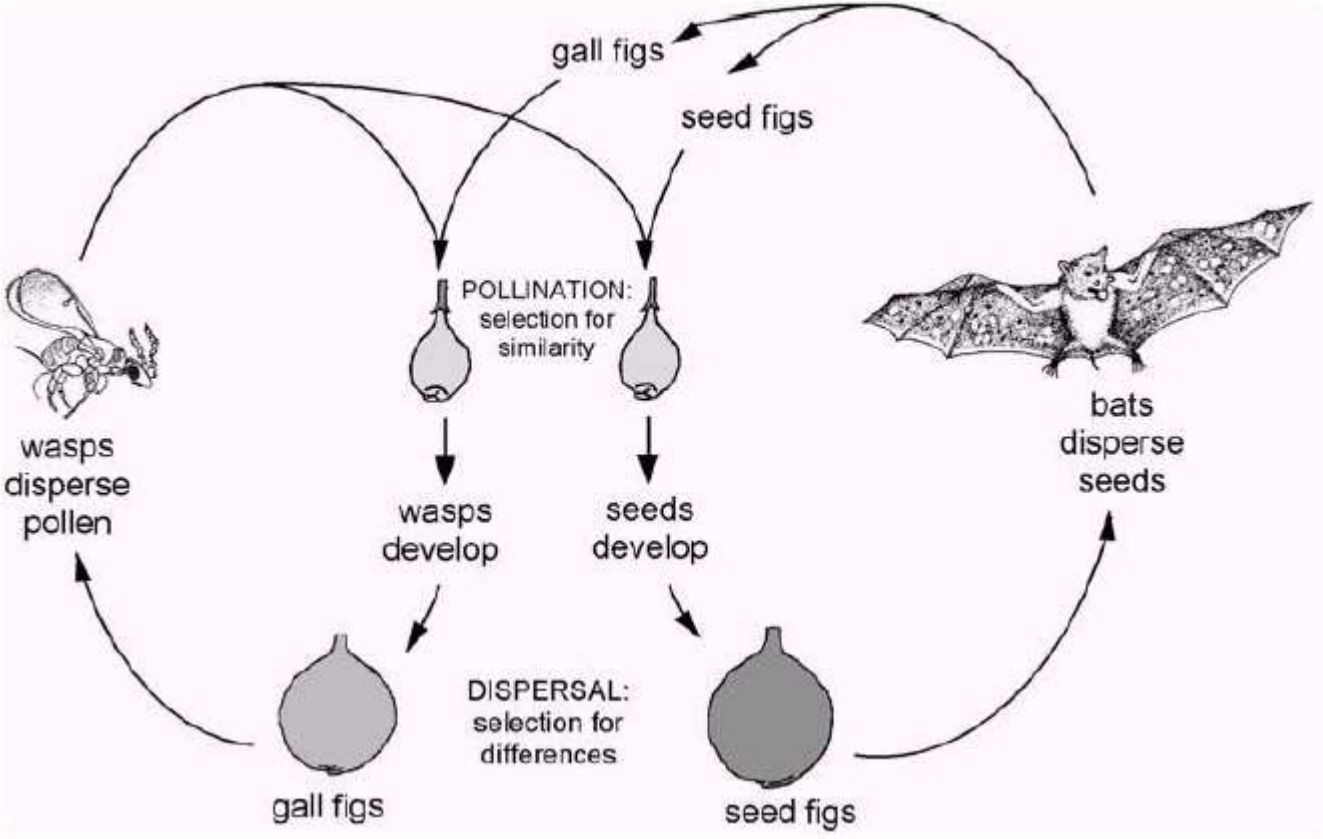
M
monoecy
D
dioecy

P
passive
pollination
A
active
pollination

Cruaud et al. *Syst. Biol.* 61(6):1029–1047, 2012

Dioecious figs: seed- and wasp-producing figs are selected to

- be indistinguishable to fig wasps at the time of pollination
- be distinct to bats when they are ripe

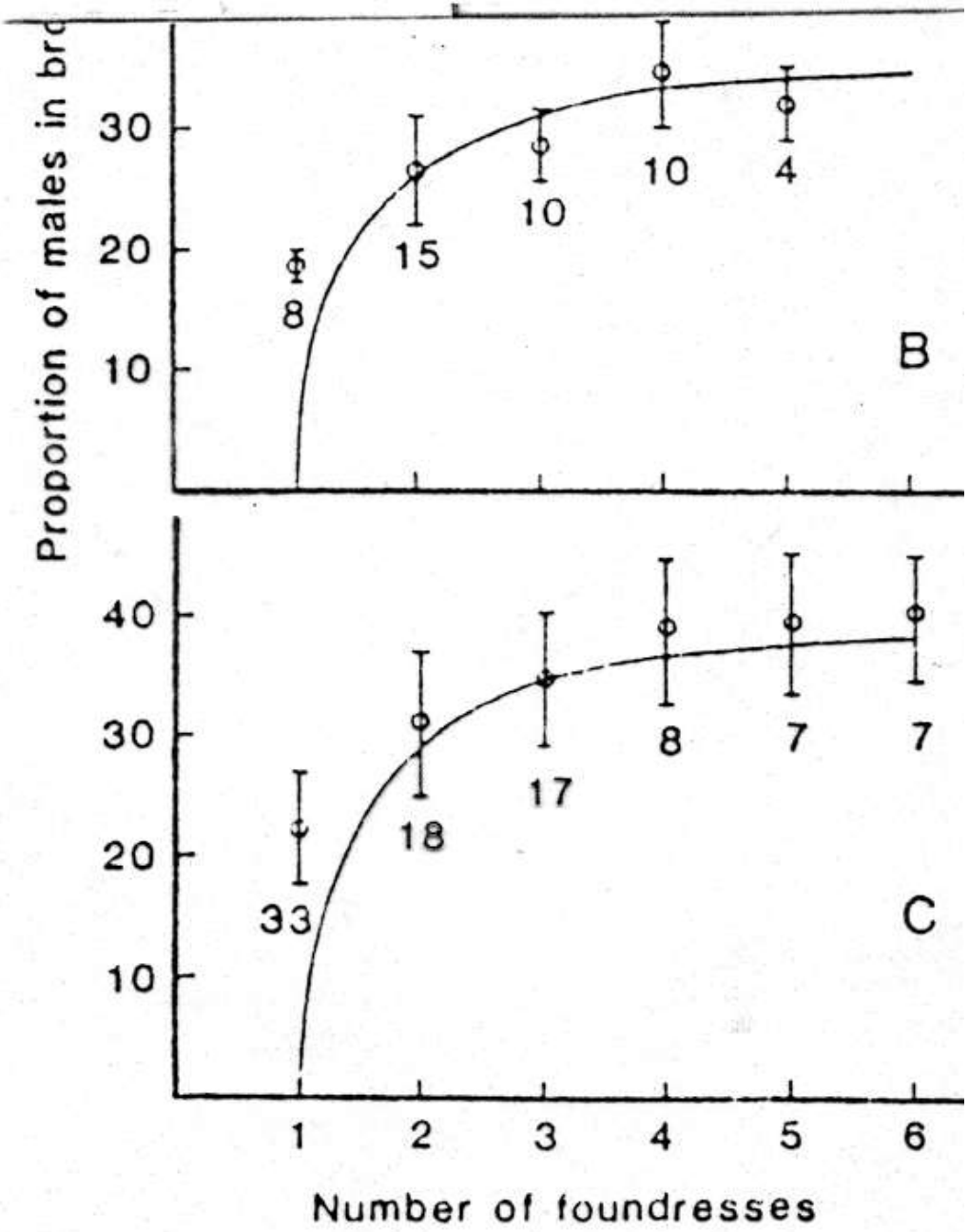


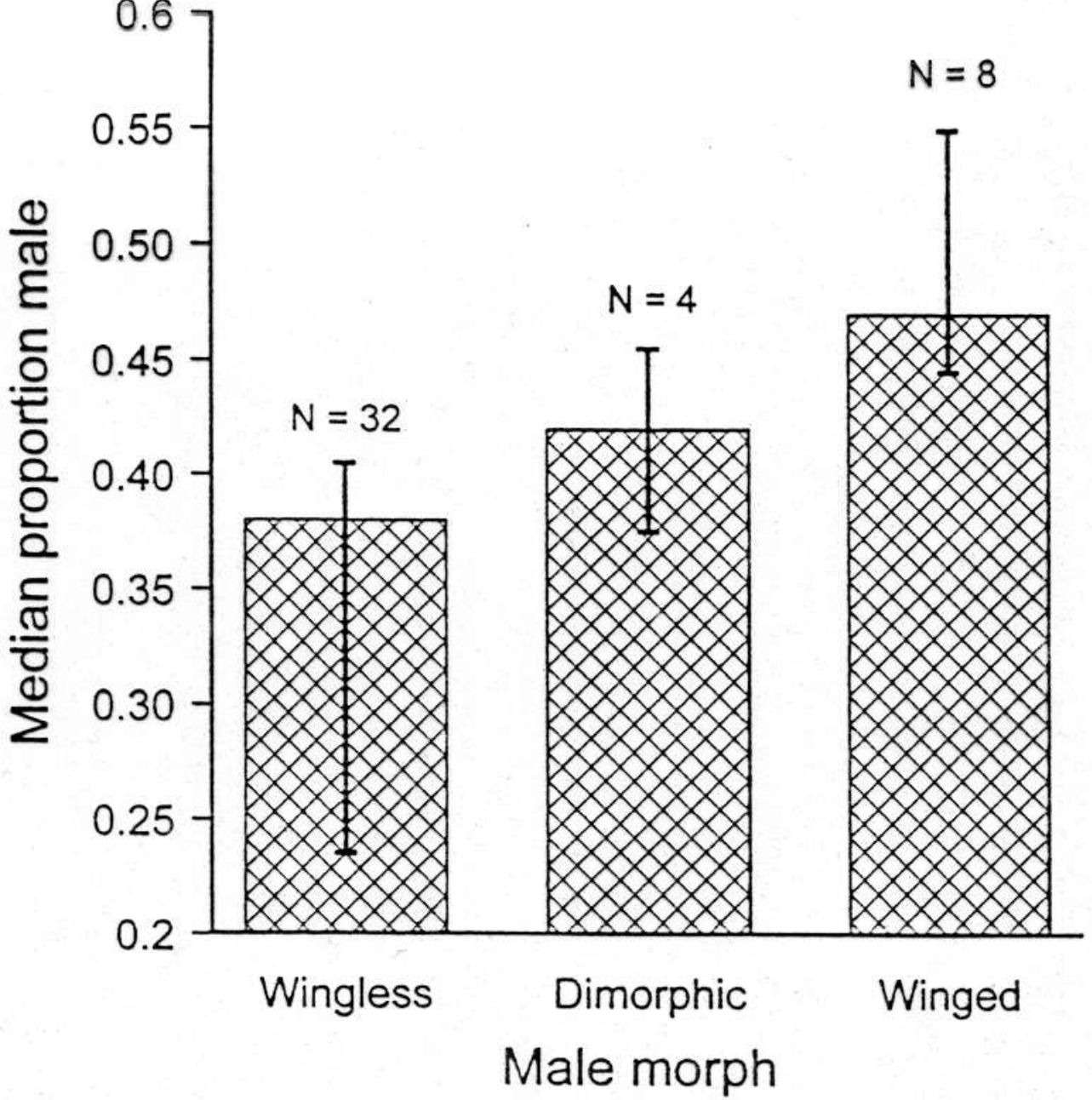
differences

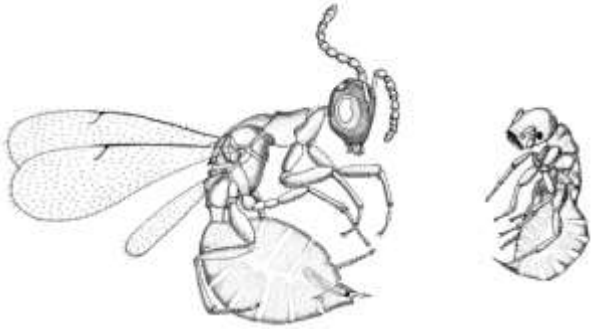
Ficus pungens

Dumont et al. 2004

Fig wasps as a model for the study of optimum sex ratios







Pseudidarnes minerva
dimorphic males

Fig. 2 Median sex ratio (± interquartiles) for fig wasp species with different male morphs

Fellowes et al. Behav Ecol Sociobiol (1999) 46: 95-102

Fig wasps as a model for the study of virulence of parasites

Virulence of nematodes infecting fig wasps

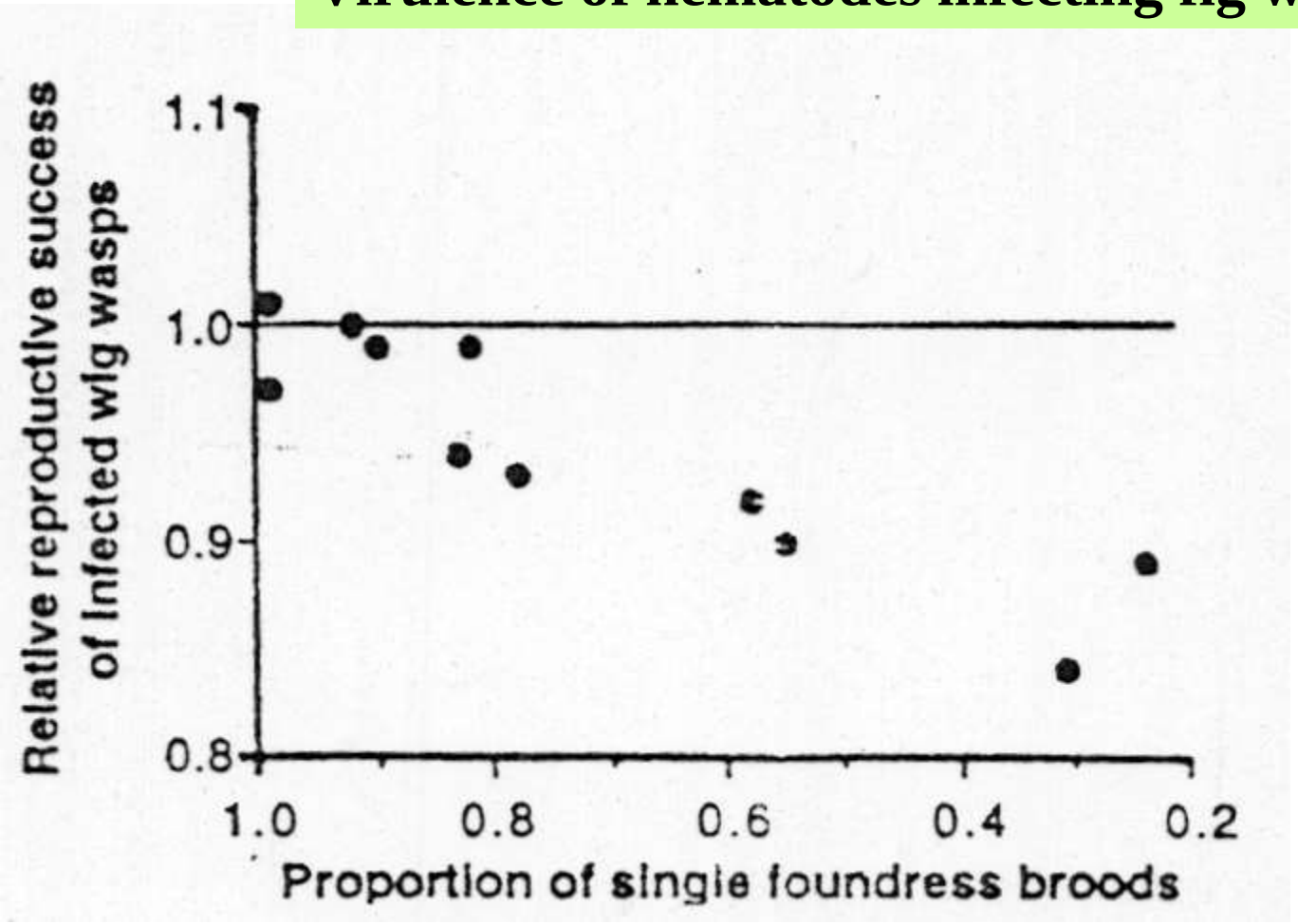


Fig. 1. Relation between virulence, measured as the lifetime reproductive success of nematode-infected relative to uninfected female fig wasps, and the proportion of multifoundress broods encountered in 11 Panamanian species. Increased incidence of multifoundress broods provides increased opportunities for nematode transmission. Those species of wasp characterized by increased opportunities for transmission of their species-specific parasitic nematodes contain more virulent species of nematodes. All statistical tests indicate a significant relation [$P < 0.001$ (*22*)].

Herre 1993: Science 259, 1442

Factors impacting the fitness of figs and fig wasps

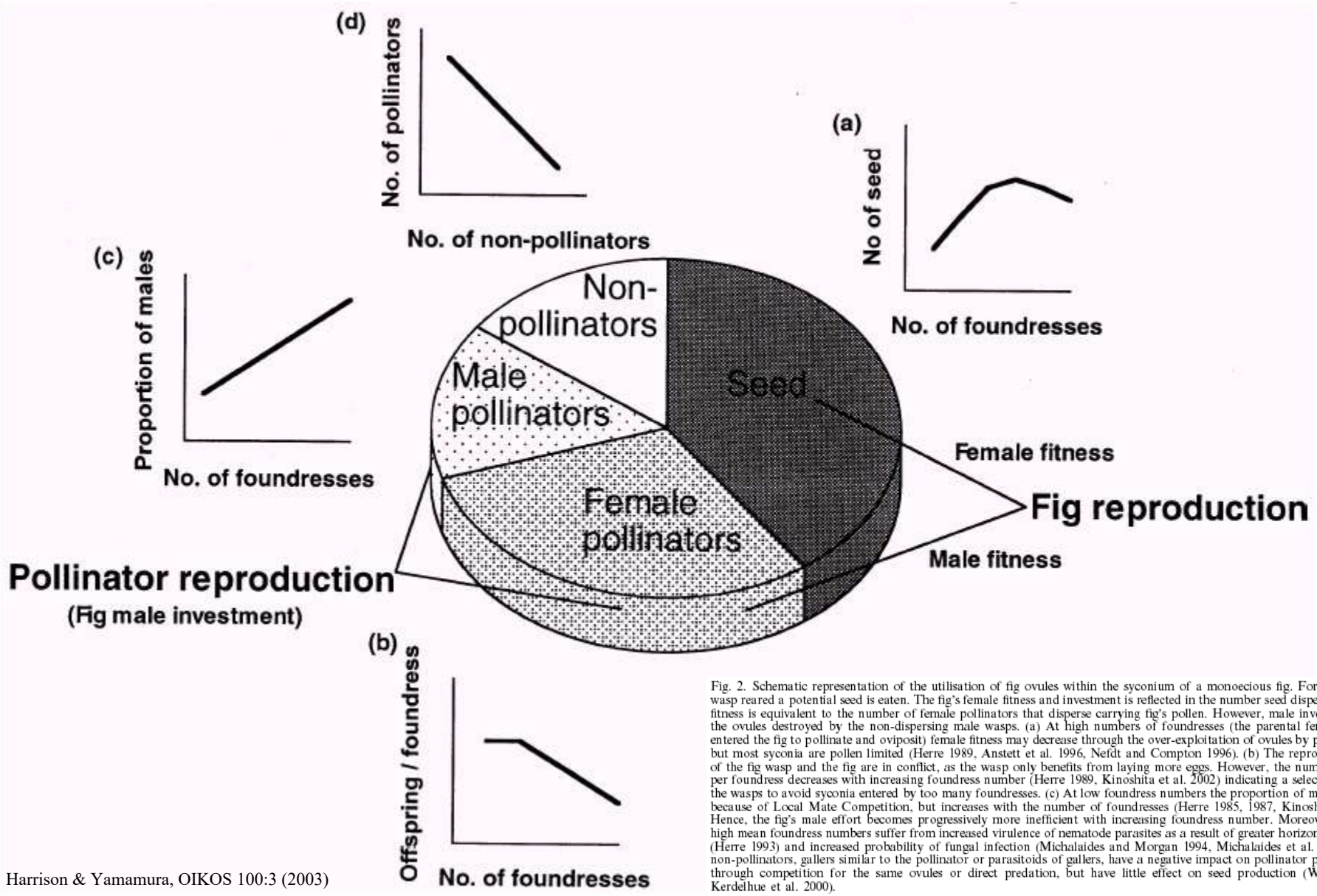


Fig. 2. Schematic representation of the utilisation of fig ovules within the syconium of a monoecious fig. For each pollinator wasp reared a potential seed is eaten. The fig's female fitness and investment is reflected in the number seed dispersed, while male fitness is equivalent to the number of female pollinators that disperse carrying fig's pollen. However, male investment includes the ovules destroyed by the non-dispersing male wasps. (a) At high numbers of foundresses (the parental female wasps that entered the fig to pollinate and oviposit) female fitness may decrease through the over-exploitation of ovules by pollinator larvae, but most syconia are pollen limited (Herre 1989, Anstett et al. 1996, Nefdt and Compton 1996). (b) The reproductive interests of the fig wasp and the fig are in conflict, as the wasp only benefits from laying more eggs. However, the number of offspring per foundress decreases with increasing foundress number (Herre 1989, Kinoshita et al. 2002) indicating a selection pressure on the wasps to avoid syconia entered by too many foundresses. (c) At low foundress numbers the proportion of male wasps is low because of Local Mate Competition, but increases with the number of foundresses (Herre 1985, 1987, Kinoshita et al. 1998). Hence, the fig's male effort becomes progressively more inefficient with increasing foundress number. Moreover, species with high mean foundress numbers suffer from increased virulence of nematode parasites as a result of greater horizontal transmission (Herre 1993) and increased probability of fungal infection (Michalaides and Morgan 1994, Michalaides et al. 1996). (d) Most non-pollinators, gallers similar to the pollinator or parasitoids of gallers, have a negative impact on pollinator production either through competition for the same ovules or direct predation, but have little effect on seed production (West et al. 1996, Kerdelhue et al. 2000).

Harrison & Yamamura, OIKOS 100:3 (2003)

What fig trees want:

- flowers pollinated
- optimum wasp infestation
- wasps entering female figs
- wasp sex ratio

females>>males

- long-distance pollen

dispersal

Fig ‘syndromes’

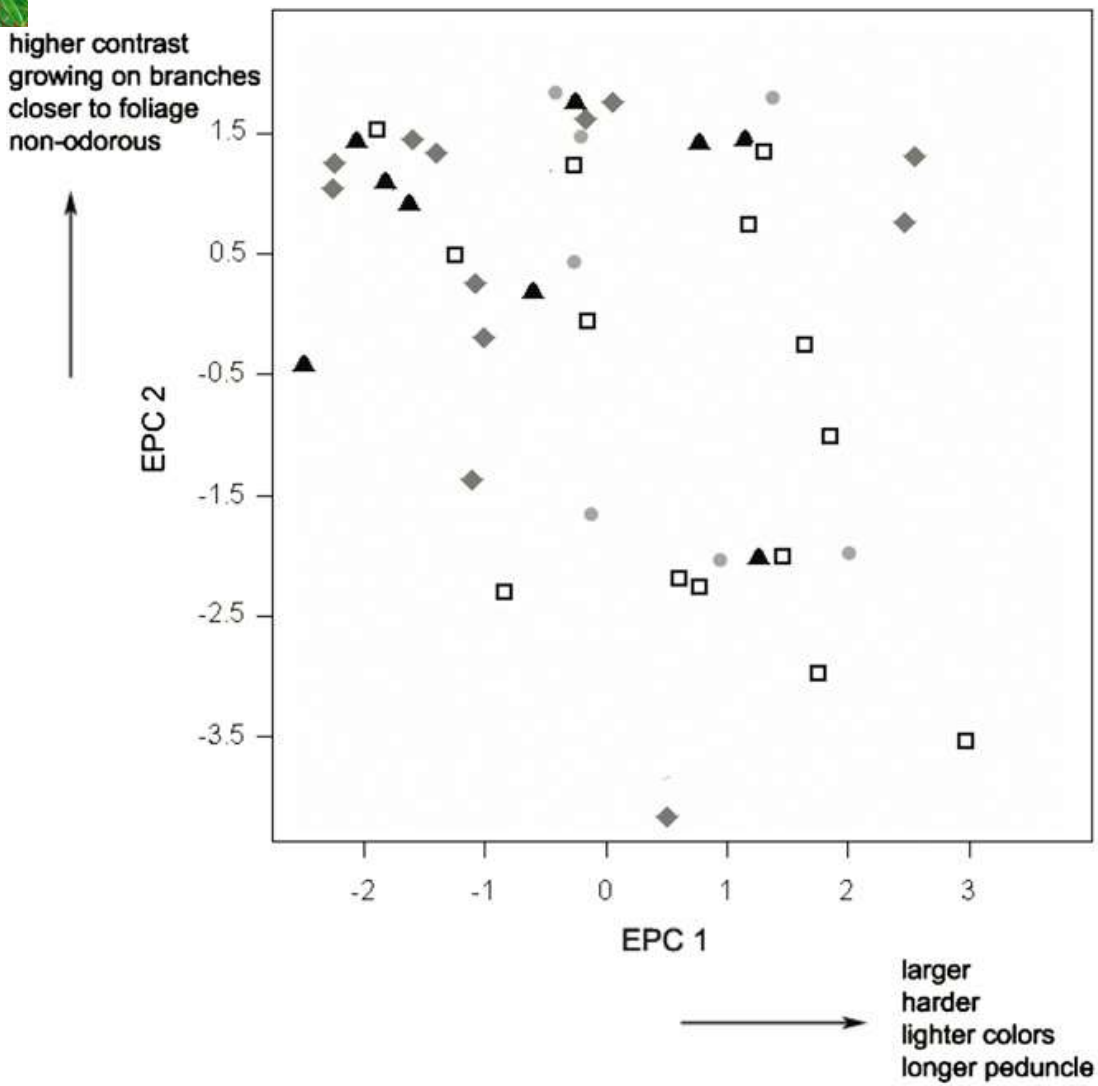
	figs	
size	small	large
colour	red	green
seed dispersal	birds	bats
clues for dispersers	visual	olfactory
wasp foundresses	few	many
wasp sex ratio	females>>males	females>males
nematodes	avirulent	virulent

Bird vs. bat dispersal syndromes

Bird syndrome

smaller
softer
darker
shorter peduncle

higher contrast
growing on branches
closer to foliage
non-odorous



lower contrast
growing from trunk
further from foliage
aromatic

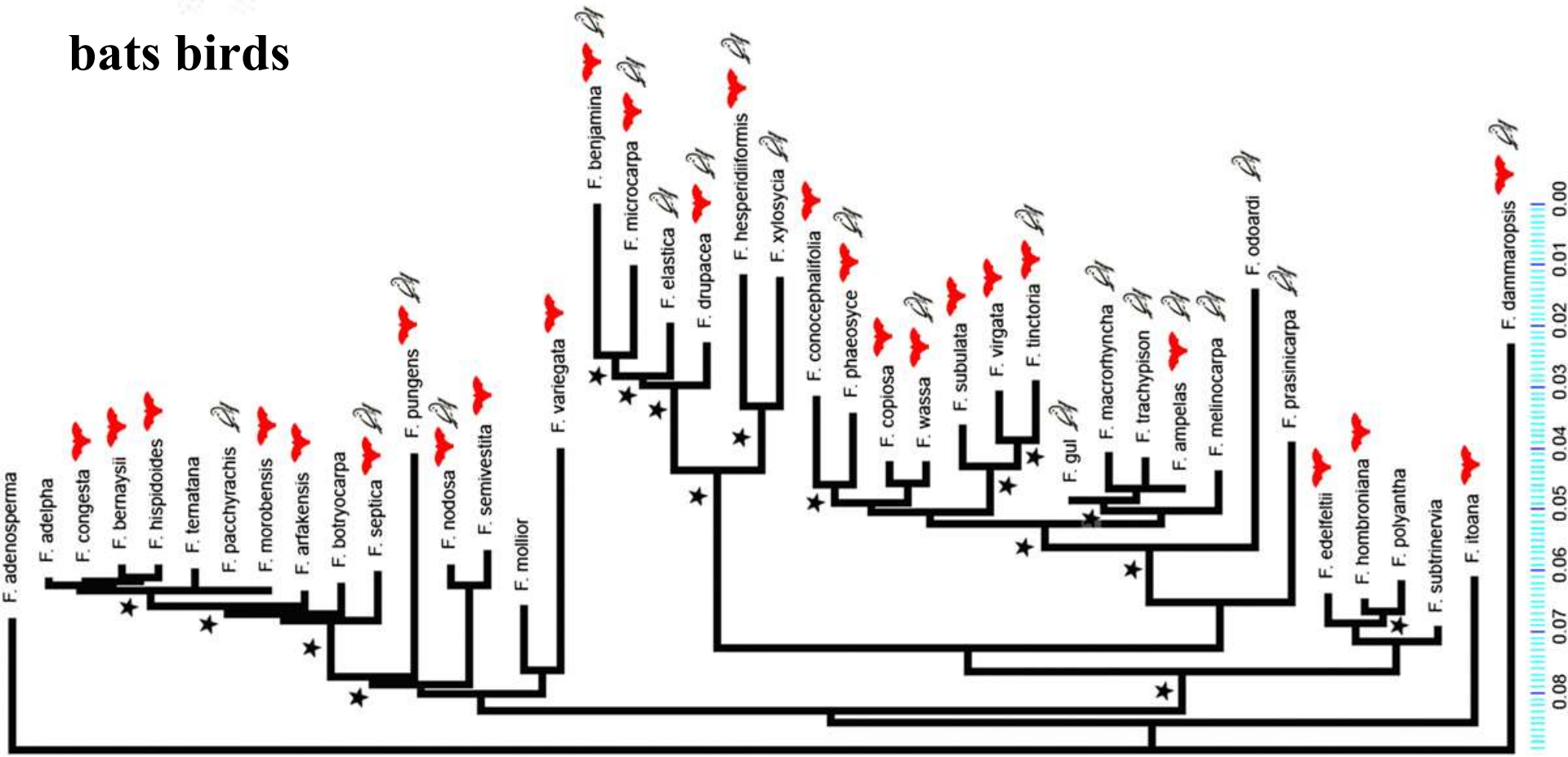
larger
harder
lighter colors
longer peduncle

Bat syndrome

Lomascolo et al PNAS 2010

Fig dispersal syndrome is evolutionarily flexible

bats birds



Lomascolo et al PNAS 2010

Figs as keystone species in some rainforest ecosystems

Fig wasps as pollinators

↓

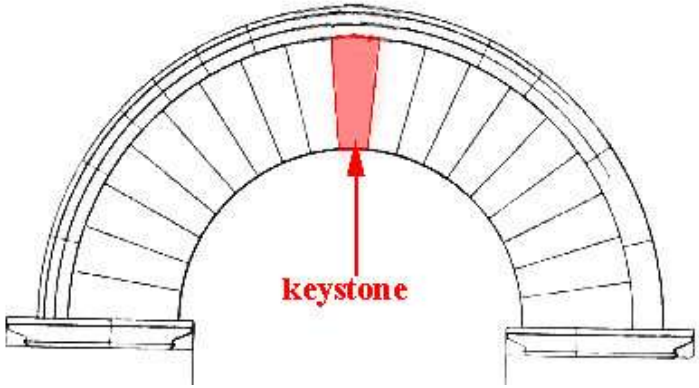
Asynchronous flowering

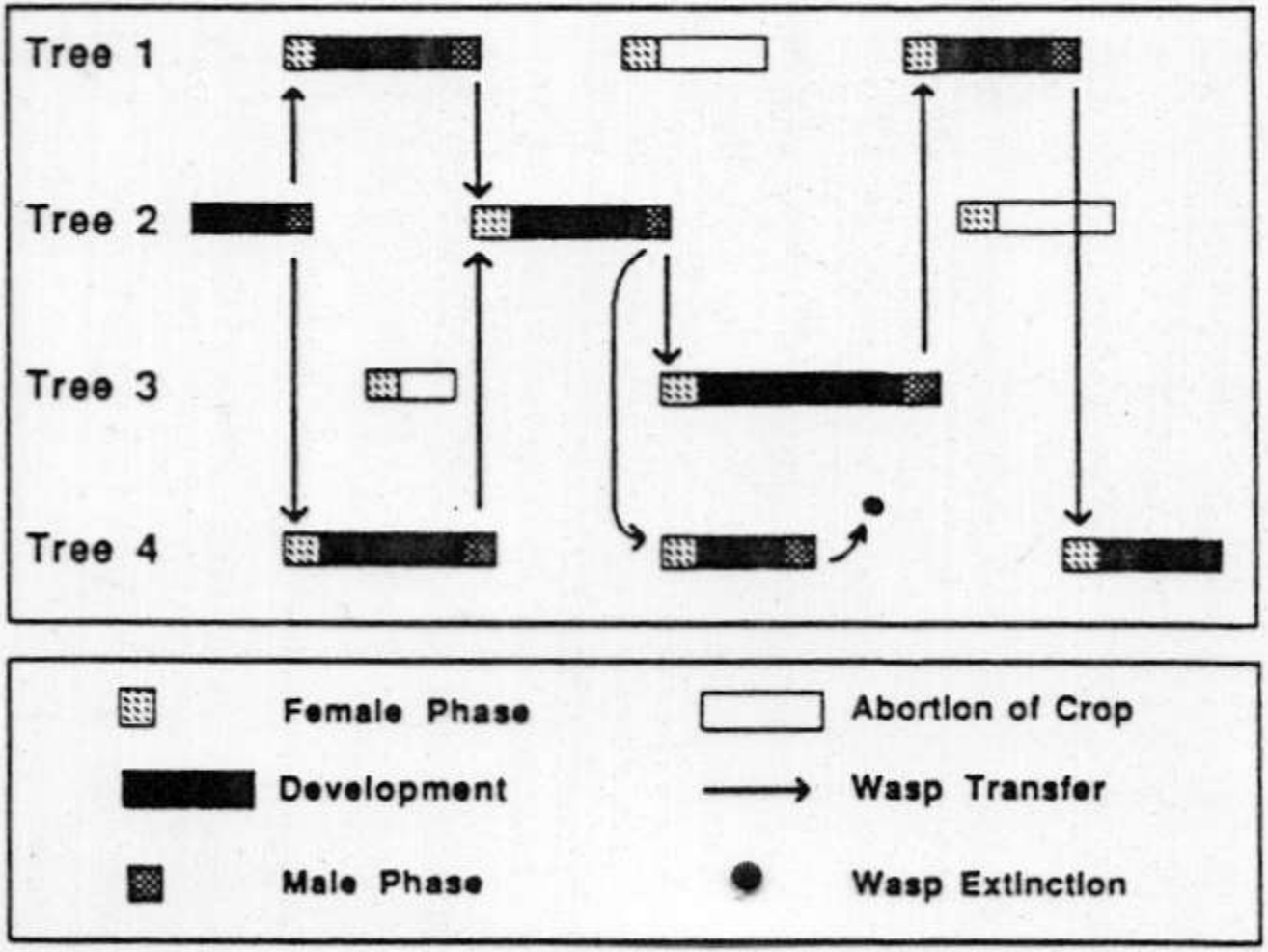
↓

Constant production of figs

↓

Key food source for frugivores





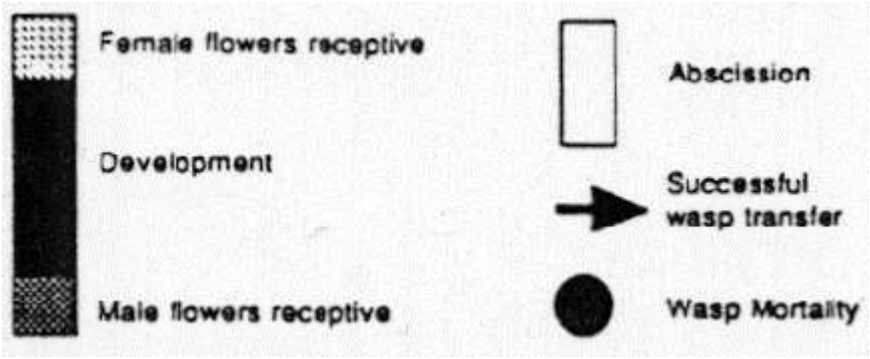
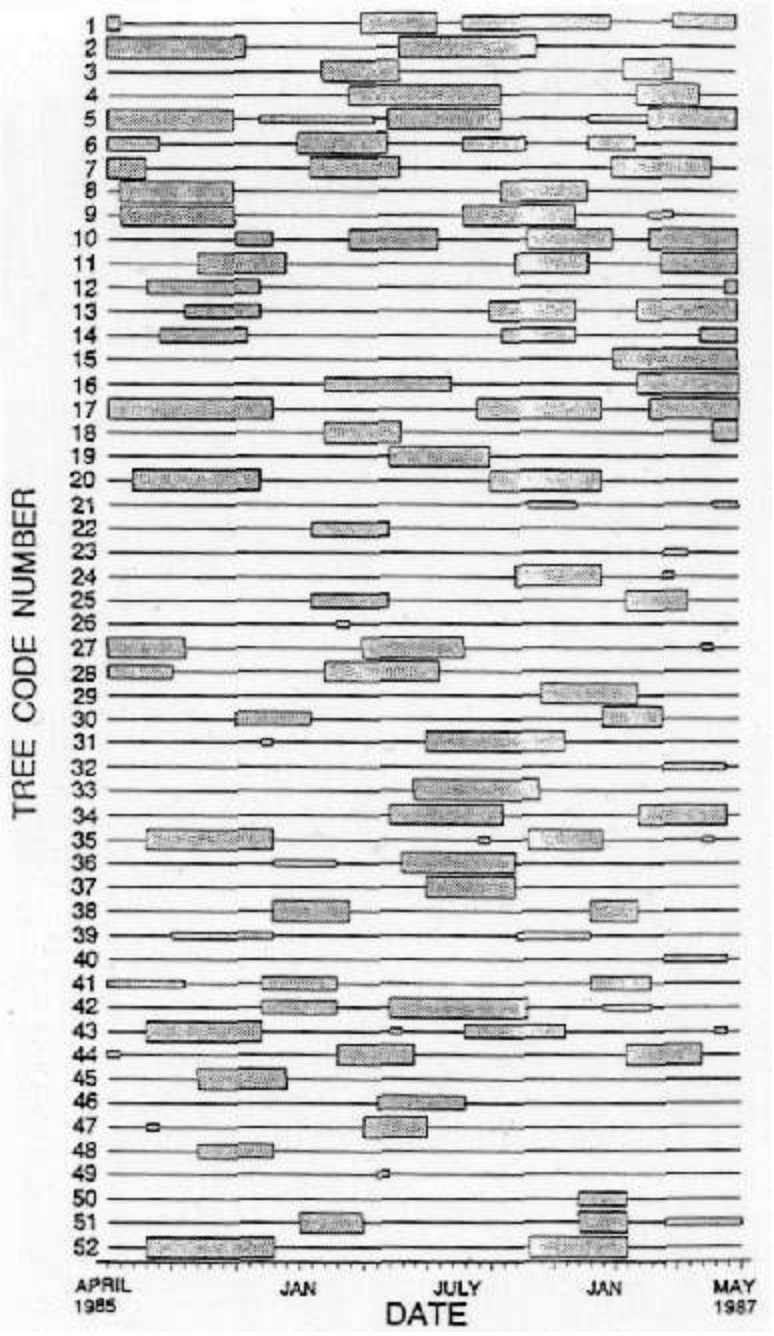


Fig wasp pollination can be maintained only by asynchronous flowering in the Ficus population

FIGURE 13. Hypothetical flowering sequence of a four-tree monoecious fig population. Note that (1) if any one of these trees were absent, the pollinator population would become locally extinct during the time period shown. (2) Although pollinators can persist in this example, there is variability in the success of individual crops: of the complete crops shown, four are successful in both the male and female phase, one is successful only in the male phase, and three are sterile.

Asynchronous fruiting in a population of 52 *Ficus burtt-davyi* trees (S. Africa)



0 The fruiting patterns of 52 *F. burtt-davyi* trees growing in Grahamstown. l crops of very short duration (for example on trees 26 and 49) aborted at an early stage of development

% of trees fruiting 1984-1985

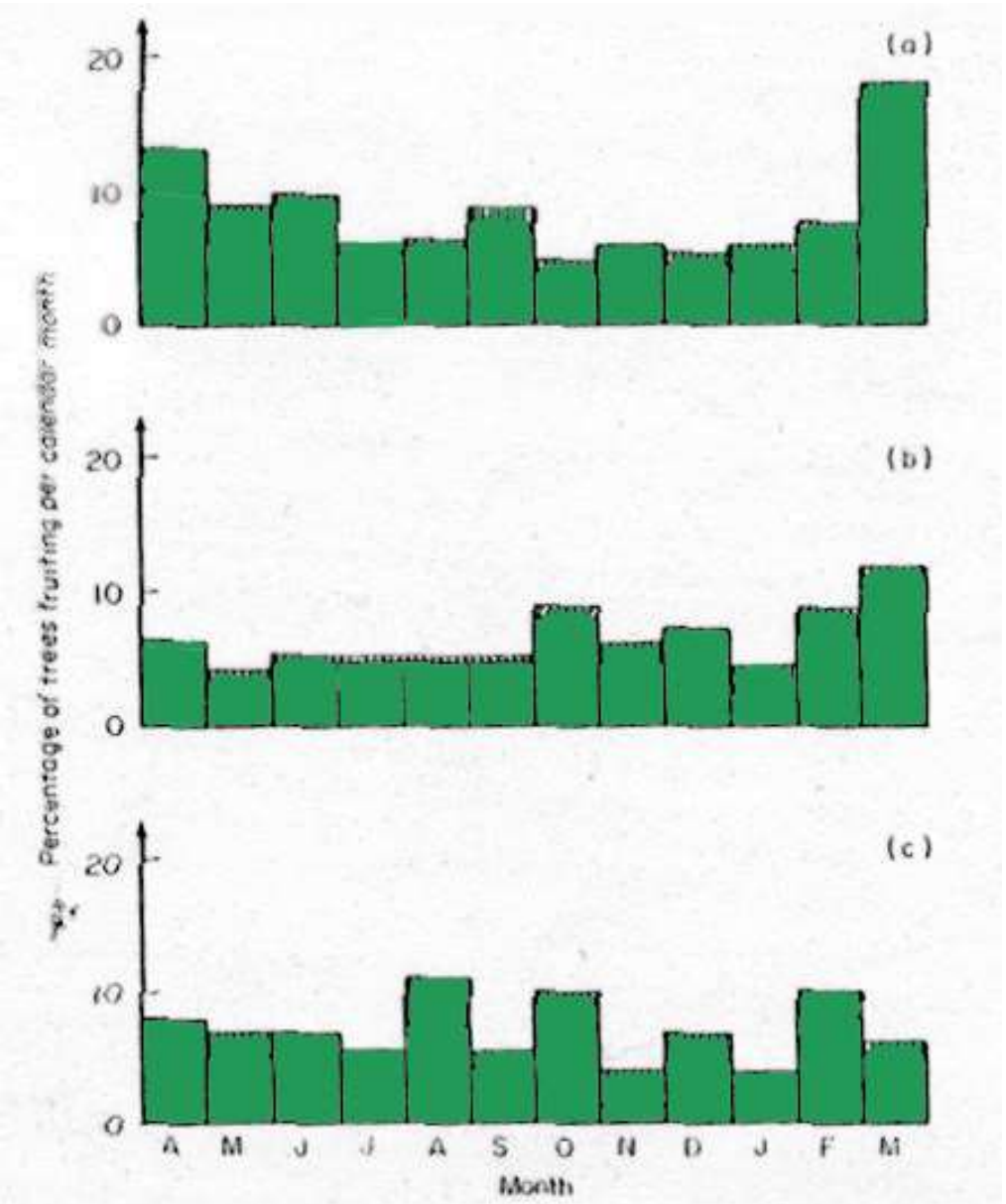
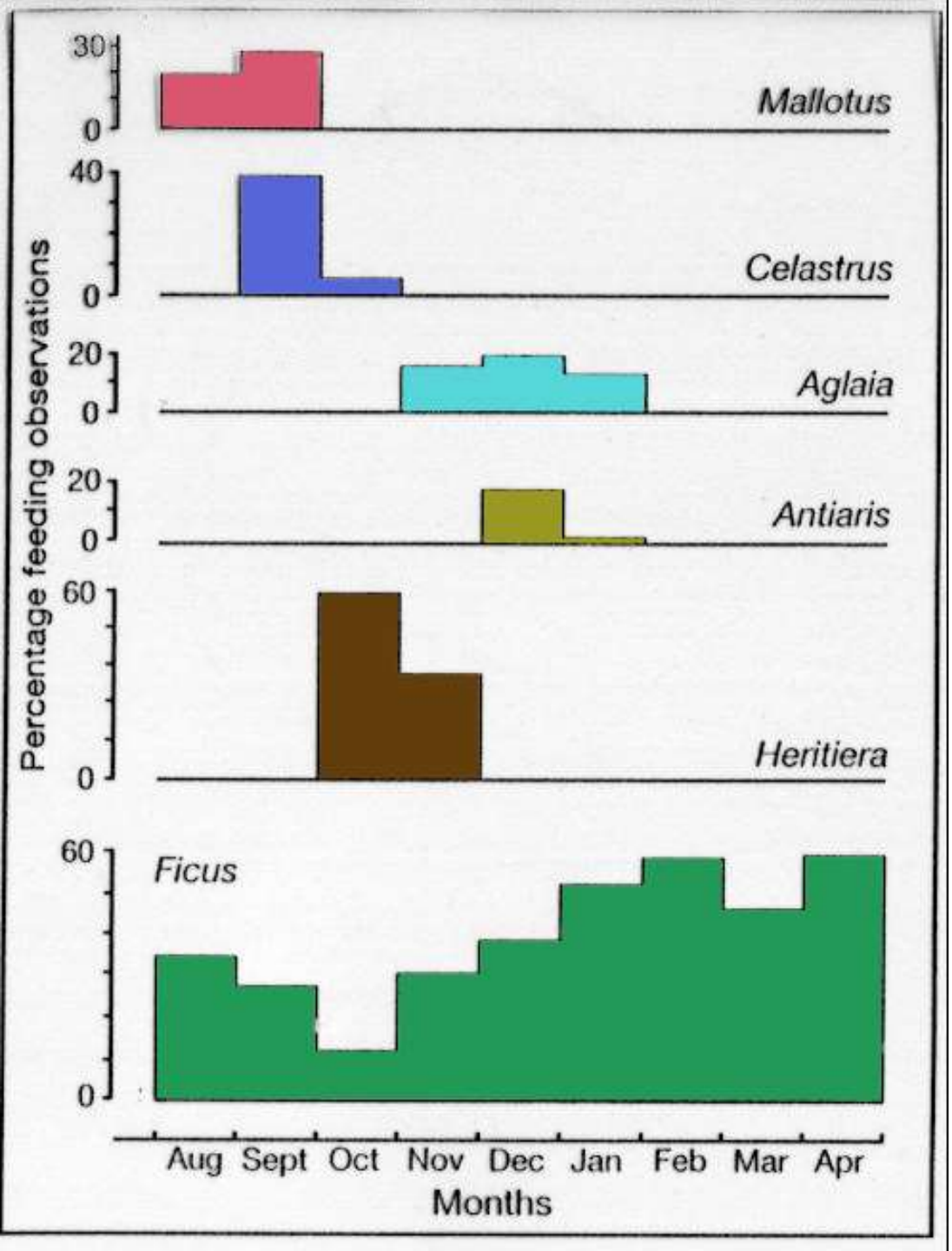


FIG. 1. Fruiting phenology of the bird-dispersed *Ficus* guild at Kuala Lompat in (a) 1984–85, (b) 1985–86 and (c) 1986–87, expressed as the percentage of trees with ripe fruit crops month^{-1}. Shading indicates the proportion contributed by minor fruitings (for definition see text). For the period June–September 1985 a mean monthly value is given.

Fruiting phenology of bird-dispersed *Ficus* spp. in a rainforest in Malaysia

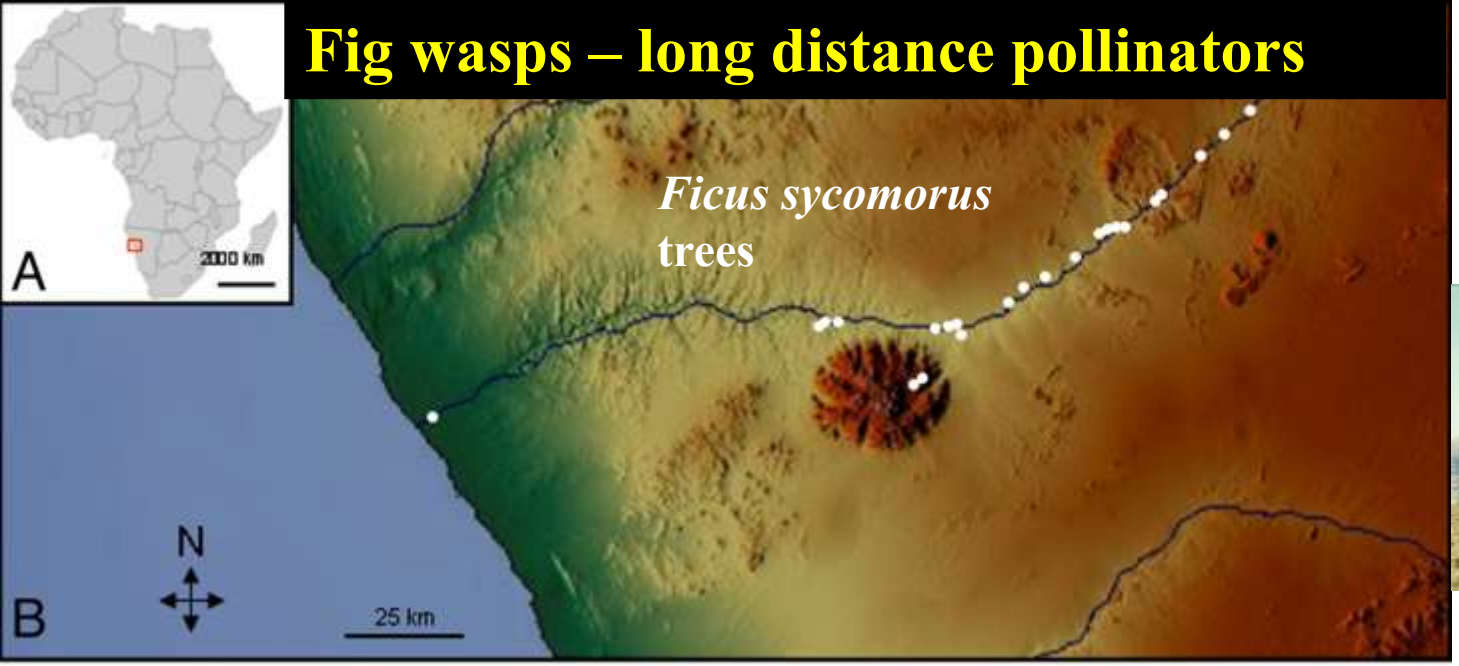


Main sources of food for orangutans in North Sumatra

Ficus - extremely efficient long-distance pollen dispersal

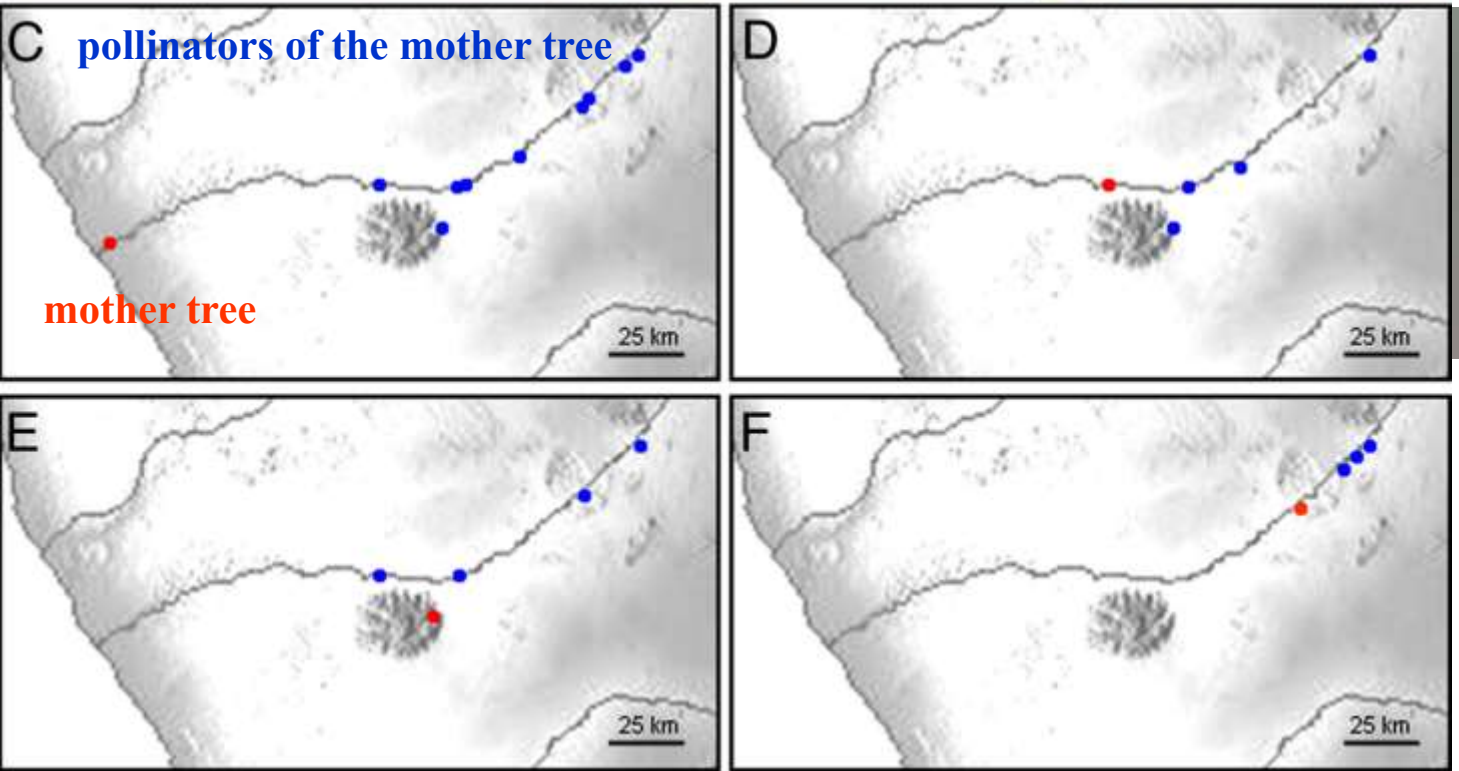
FICUS	OBTUSIFOLIA	POPENOEI
TREE DENSITY /HA	14	76
WASP-PRODUCING TREES /HA	0.003	0.0005
PARENT TREES	17	6
SOURCE AREA HA	6,198	11,856

Fig wasps – long distance pollinators



Mean observed pollination distance 89 km, maximum 165 km

Ficus sycomorus



Ceratosolen arabicus

Ahmed et al. 2009, PNAS 106: 20342–20347

(*A*) Position of the field site in Namibia, Southern Africa. (*B*) Distribution of adult trees. Paternity assignments relating to individual female parents (*red*) and assigned pollen donors (*blue*)

Fig trees - good colonisers. The Krakatoa example:

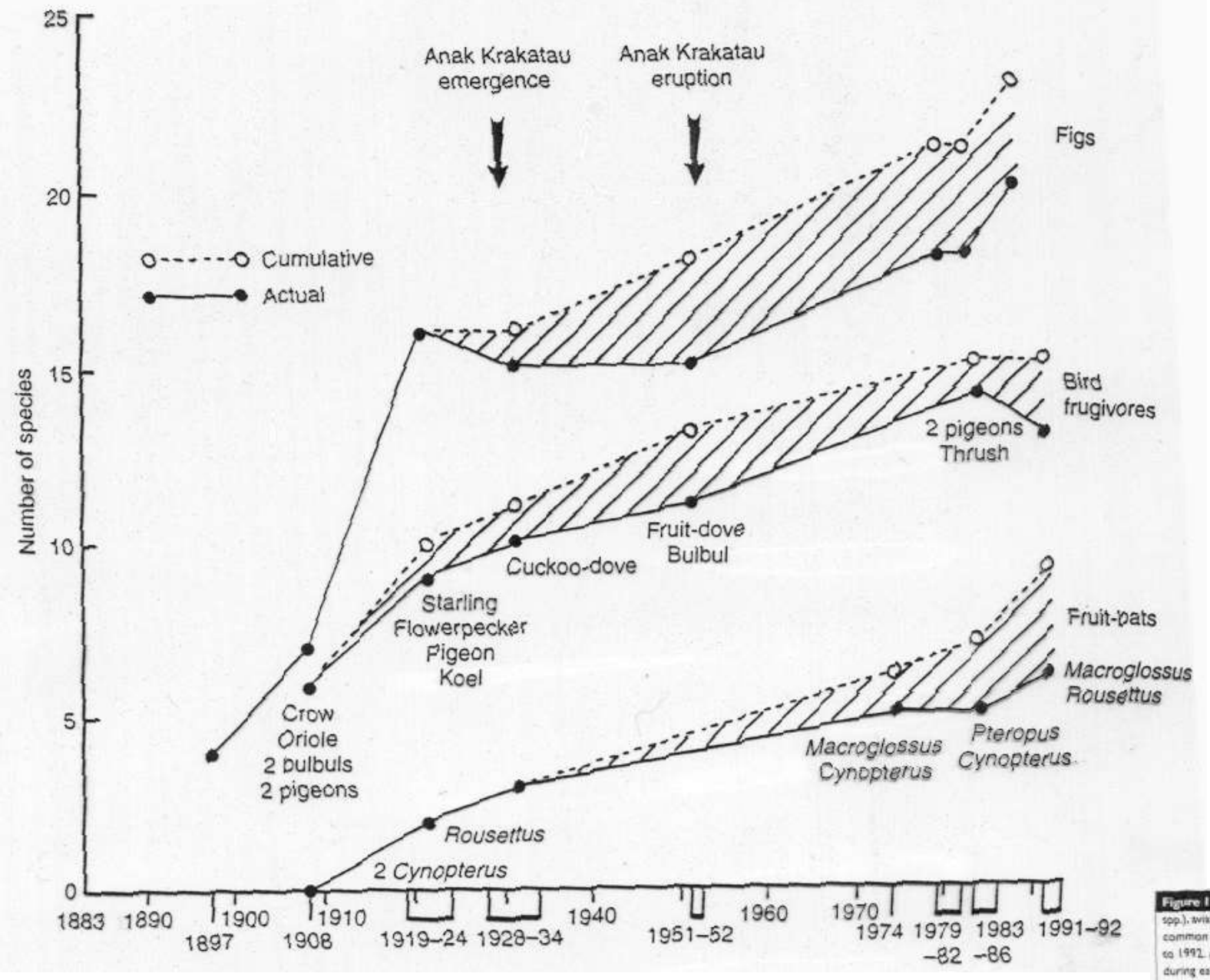
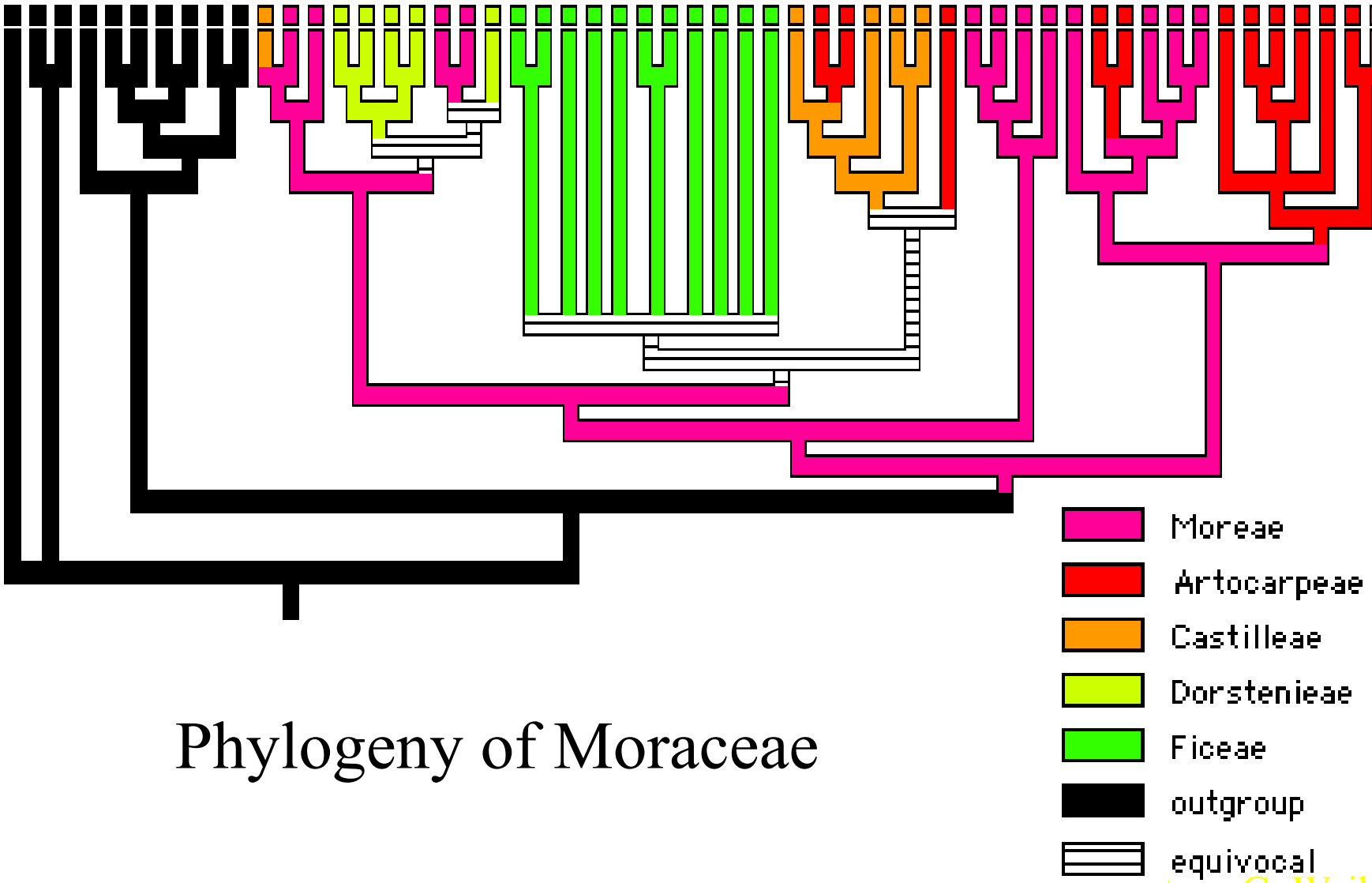


Figure 12.4 Colonization of the Krakatau by figs (*Ficus* spp.), avian frugivores (indicated at date of first record by common name) and fruit-bats (by generic name), from 1883 to 1992. Actual line plots the number of species recorded during each survey period, and the cumulative line is the number of species recorded by each survey plus those recorded previously and not seen during a particular survey (after Thornton 1996. Reprinted by permission of the

How the fig - wasp mutualism evolved?

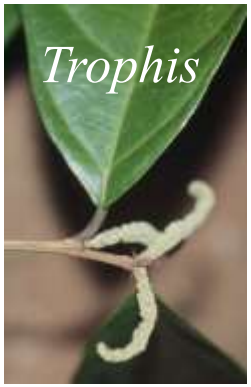


Phylogeny of Moraceae

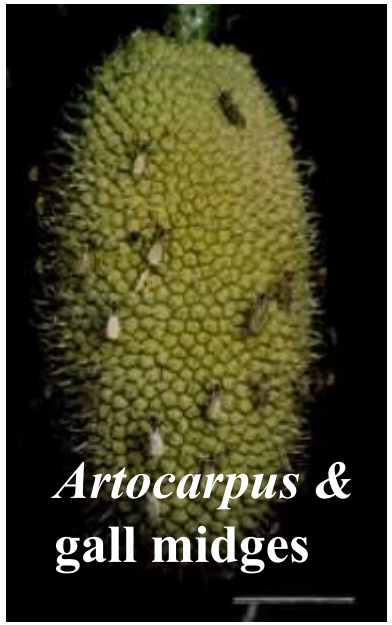
courtesy G. Weiblen

Moraceae: pollination syndromes

wind pollination

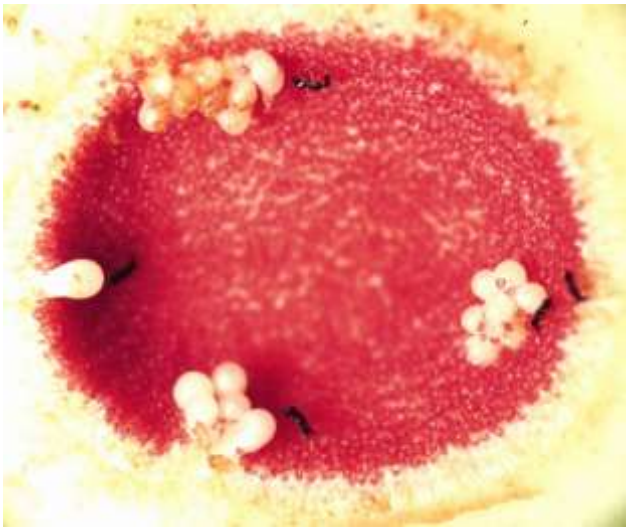


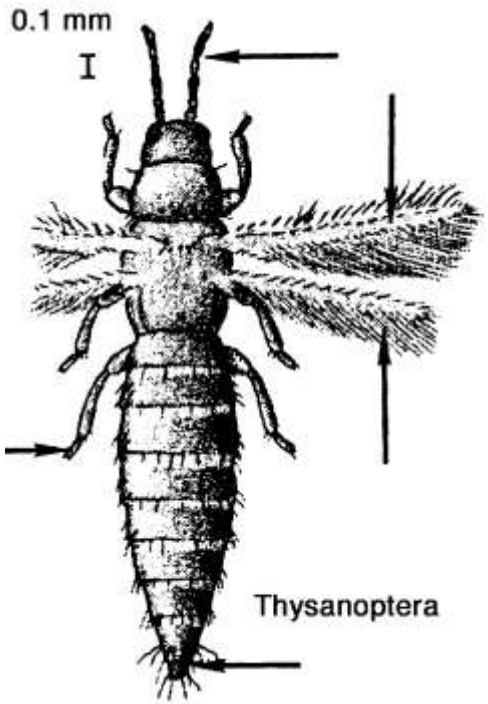
insect pollination

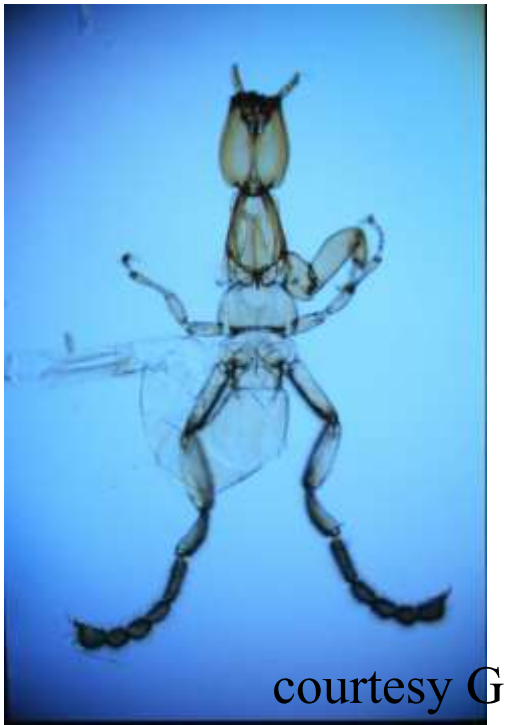


Courtesy G. Weiblen

Castilleae & Ficeae: insect pollination in sister lineages







courtesy G. Weiblen

The plant - insect mutualisms where
• the insect pollinates flowers
• then oviposits to some of them so that the larval survival depends on successful pollination
are among few cases of genuine coevolution between plants and insects.

Ficus - Agaonidae wasps

Yucca - Tegeticula moths (Yponomeutidae)

Trollius - Chiastocheta (Anthomyiidae) flies

Glochidium - Epicephala (Gracillariidae) moths

Yucca plants - *Tegeticula* moths

Yucca moths: cheaters in the mutualistic clade

obligate pollinators

cheaters – depend on pollination by other spp., only oviposit in flowers, early or late in flower development

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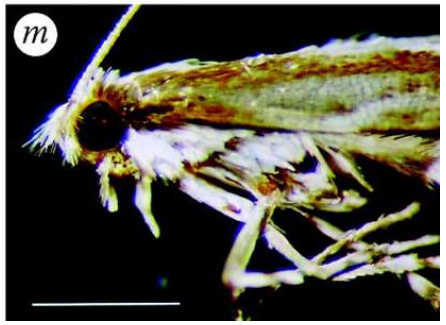
Pathways to mutualism breakdown

Joel L. Sachs and Ellen L. Simms

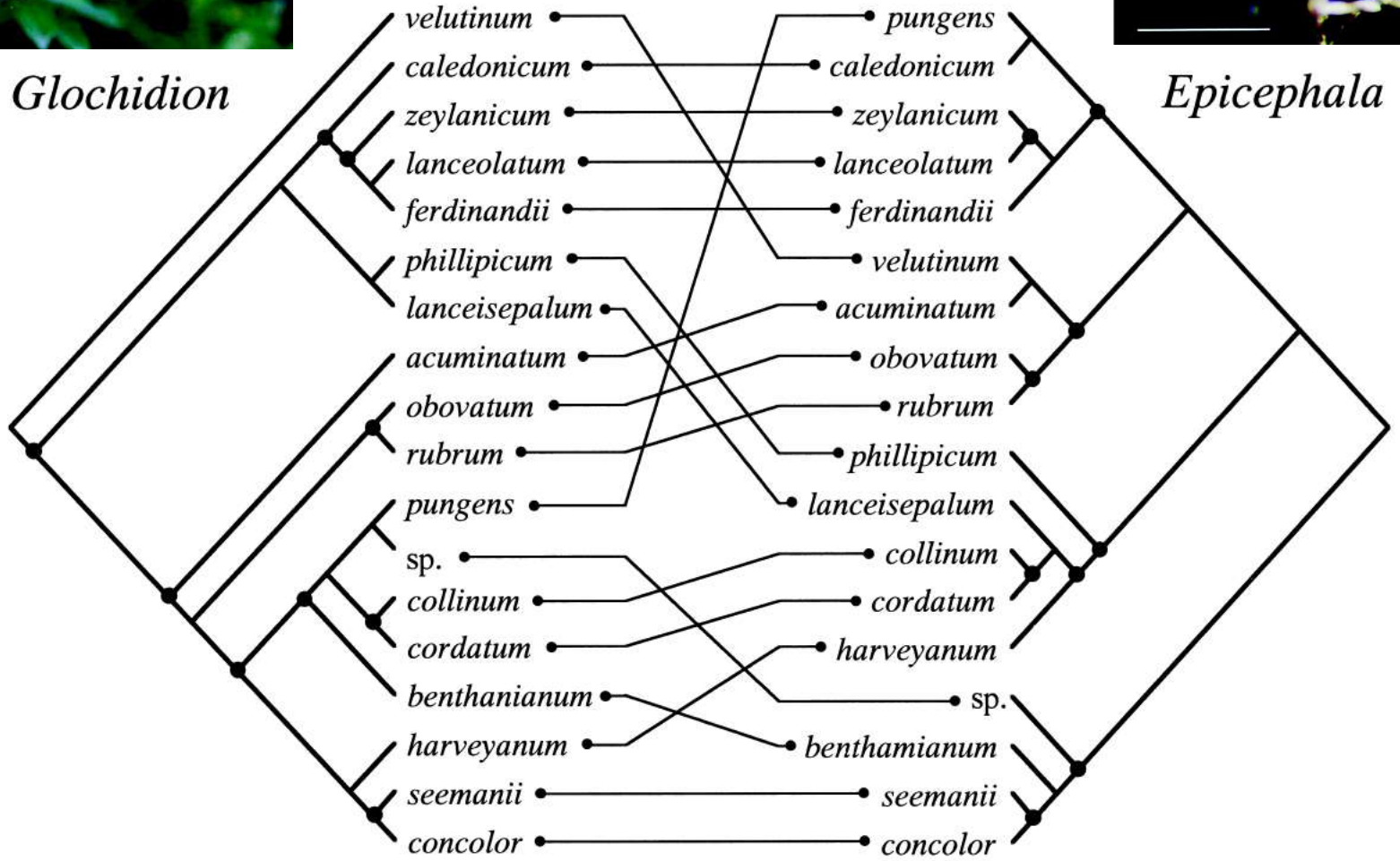
Epicephala sp. (Gracillariidae) and Glochidium (Euphorbiaceae)

Kato et al. 2003. PNAS 100:5264

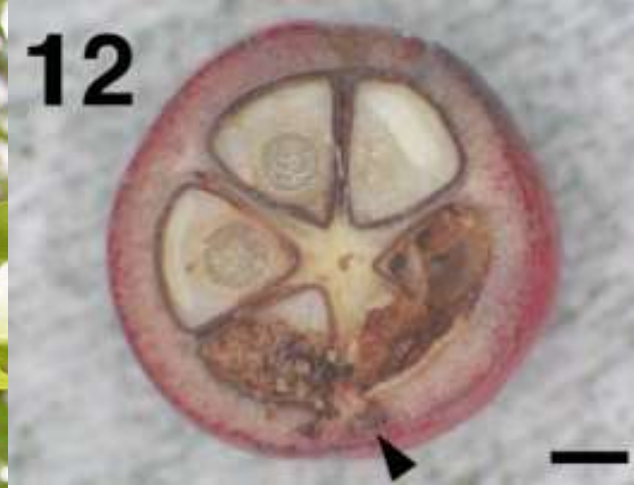


Glochidion

Epicephala



Kawakita et al., Evolution, 58(10), 2004, pp. 2201–2214



Kawakita & Kato, American Journal of Botany 91(9): 1319–1325. 2004

Epicephala (Gracillariidae) on *Breynia* (Euphorbiaceae)



Kawakita & Kato, American Journal of Botany 91(3): 410–415. 2004

Epicephala (Gracillariidae) on *Phyllanthus* (Euphorbiaceae)