TAXONOMY OF SOME FIGS AND THEIR INTERACTIONS WITH POLLINATORS

YAOWANIT TARACHAI

DOCTOR OF PHILOSOPHY
IN BIODIVERSITY AND ETHNOBIOLOGY

THE GRADUATE SCHOOL
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EXAMINING COMMITTEE

P. Chantaramongkol ....CHAIRPERSON
Assoc. Prof. Dr. Porntip Chantaramongkol

C. Trisonthi ....MEMBER
Assoc. Prof. Dr. Chusie Trisonthi

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Mr. Prachaval Sukumalanand

Prasit W. ....MEMBER
Asst. Prof. Dr. Prasit Wangpakapattanawong

Prachaya Srisanga ....MEMBER
Dr. Prachaya Srisanga

15 September 2008

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Yaowanit Tarachai

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Author Mrs. Yaowanit Tarachai

Degree Doctor of Philosophy (Biodiversity and Ethnobiology)

Thesis Advisory Committee

Assoc. Prof. Dr. Chusie Trisonthi	Chairperson
Mr. Prachaval Sukumalanand	Member
Asst. Prof. Dr. Prasit Wangpakapattanawong	Member

ABSTRACT

During taxonomic and ecological studies on figs (*Ficus* spp., Moraceae) in Chiang Mai Province, northern Thailand, from June 2005 to May 2007, 26 species of figs belonging to 6 subgenera were found. The largest subgenus, *Urostigma*, had 11 species, followed by *Sycomorus* with 8 species, *Ficus*, *Sycidium* and *Synoecia* each with 2 species and *Pharmacosycea* with 1 species. *F. benjamina* L., *F. hispida* L. and *F. racemosa* L. had each 2 varieties, but *F. fistulosa* Reinw. ex. Bl. had only 2 forms. *F. benjamina*, *F. hispida* and *F. racemosa* were common from 310-1,200 m asl., *F. anastomosans* (Corner) Berg and *F. anserina* Corner were adapted to limestone.

A large number of fig wasps were detected in every syconium, but only one species functioned as pollinator. Pollinators were identified to 20 species from the Agaonidae family. *Ceratosolen emarginatus* Mayr occurred in both *F. auriculata* Lour. and *F. oligodon* Miq. The pollinators of *F. anserina*, *F. curtipes* Corner, *F. rumphii* Bl., *F. pumila* L. and *F. maclellandii* King could not be found.

In the monoecious fig *F. racemosa* the pollinator was *C. fusciceps* Mayr. 3 species of *Platyneura* and 2 of *Apocrypta* occurred in *F. racemosa* but were not pollinators. There were 8 fruit crops in 13 months (September 2006-September 2007), 4 each in the dry and the rainy season. The number of figs and male wasp offspring

were not significantly different between the dry and rainy season, but the average number of seeds in the rainy season was higher than in the dry season, while in pollinators the progeny number was higher in dry season.

The dioecious *F. montana* Burm. f. was pollinated by *Liporrhopalum tentacularis* (Grandi). In experiments, it was found that the reproductive success (number of progeny) of females that carried pollen was twice as high as that of females that did not carry pollen. Figs entered by pollen-free fig wasps were more likely to abort. When pollen-carrying females were prevented from ovipositing by having the tips of their ovipositors removed, all the figs aborted. This suggests that either the male fig may require oviposition for gall development or the behavioral changes in the female pollinator prevented pollination due to their inability to oviposit.

ชื่อเรื่องวิทยานิพนธ์ อนุกรมวิธานของมะเดื่อบางชนิดและปฏิสัมพันธ์กับแมลงพาหะถ่ายเรณู

ผู้เขียน นางเยาวนิตย์ ธาราฉาย

ปริญญา วิทยาศาสตรดุษฎีบัณฑิต

(ความหลากหลายทางชีวภาพและชีววิทยาชาติพันธุ์)

คณะกรรมการที่ปรึกษาวิทยานิพนธ์

รศ. ดร. ชูศรี ไตรสนธิ	ประธานกรรมการ
นายปรัชวาล สุกุมลนันทน์	กรรมการ
ผศ. ดร. ประสิทธิ์ วังภคพัฒนวงศ์	กรรมการ

บทคัดย่อ

การศึกษาอนุกรมวิธานและนิเวศวิทยาของพืชสกุลมะเดื่อระหว่างเดือนมิถุนายน 2548-พฤษภาคม 2550 ในจังหวัดเชียงใหม่ พบพืชสกุลมะเดื่อ 26 ชนิดจาก 6 สกุลย่อย กลุ่มที่พบมากที่สุดมีจำนวน 11 ชนิด อยู่ในสกุลย่อย *Urostigma* รองลงมาคือ *Sycomorus* 8 ชนิด ใน *Ficus* *Sycidium* และ *Synoecia* พบสกุลย่อยละ 2 ชนิด ส่วน *Pharmacosycea* พบเพียง 1 ชนิด ชนิดที่พบ 2 สายพันธุ์ได้แก่ ไทรย้อยใบแหลม (*F. benjamina* L.) มะเดื่อปล้อง (*F. hispida* L.) และมะเดื่ออุทุมพร (*F. racemosa* L.) ชนิดที่พบสอง forms คือ ซิ้ง (*F. fistulosa* Reinw. ex. Bl.)

พืชสกุลมะเดื่อบางชนิดมีการกระจายพันธุ์ตั้งแต่ระดับความสูง 310 ถึง 1,200 เมตรเหนือระดับน้ำทะเล เช่น ไทรย้อยใบแหลม มะเดื่อปล้องและมะเดื่ออุทุมพร ในขณะที่บางชนิดกระจายพันธุ์ในพื้นที่ค่อนข้างเฉพาะ เช่น *F. anserina* Corner และ *F. anastomosans* (Corner) Berg พบเฉพาะพื้นที่เขาหินปูน จำนวนแมลงที่อาศัยร่วมกับช่อดอกและผลของพืชสกุลมะเดื่อมีจำนวนมาก แต่มีเพียงหนึ่งชนิดที่ทำหน้าที่เป็นแมลงพาหะถ่ายเรณู (pollinator) จากการศึกษาจำแนกแมลงที่เป็น

พาหะถ่ายเรณูได้ 20 ชนิด ซึ่งทั้งหมดเป็นแมลงในวงศ์แตนมะเดื่อ (Agaonidae) จากการสำรวจมีมะเดื่อ 2 ชนิดได้แก่เดื่อหว้า (*F. auriculata* Lour.) และเดื่อหลวง (*F. oligodon* Miq.) มีแตนชนิดเดียวกันผสมเกสรคือ *Ceratosolen emarginatus* Mayr ในการศึกษาไม่พบแตนผสมเกสรในพืช 5 ชนิด ได้แก่ *F. anserina, F. curtipes* Corner, ไพขี้นก (*F. rumphii* Bl.), เดื่อเถา (*F. pumila* L.) และ ไทร (*F. maclellandii* King)

การศึกษาการผสมเกสรของมะเดื่ออุทุมพร ซึ่งเป็นชนิดแยกเพศร่วมต้น (monoecious) กับแตนผสมเกสรคือ *C. fusciceps* Mayr พบแตนกลุ่มอื่นที่ไม่ใช่พาหะถ่ายเรณูจำนวน 5 ชนิดได้แก่ สกุล *Apocrypta* 2 ชนิดและ *Platyneura* (*Apocryptophagus*) 3 ชนิด เมื่อสังเกตการติดผลของประชากรมะเดื่ออุทุมพรพบว่าในระยะ 13 เดือนที่ศึกษาวิจัย (กันยายน 2549-กันยายน 2550) ติดผล 8 ครั้ง โดยติดผลช่วงฤดูแล้ง 4 ครั้งและฤดูฝน 4 ครั้ง ระหว่างฤดูแล้งและฤดูฝนการผลิตช่อดอกและผลกับจำนวนแมลงพาหะถ่ายเรณู มีความแตกต่างกันอย่างไม่มีนัยสำคัญทางสถิติ ส่วนจำนวนเมล็ดมะเดื่อในฤดูฝนมีค่าเฉลี่ยสูงกว่าในฤดูแล้ง ในขณะที่จำนวนลูกของแมลงในช่วงฤดูแล้งมีค่าเฉลี่ยมากกว่าช่วงฤดูฝน

การศึกษาความสัมพันธ์ระหว่างมะเดื่อชนิดแยกเพศต่างต้นกับแตนผสมเกสร ศึกษาทดลองในมะเดื่อหิน (*F. montana* Burm.f.) กับแตนมะเดื่อ *Liporrhopalum tentacularis* (Grandi) พบว่าช่อดอกมะเดื่อเพศผู้ที่ได้รับการผสมเกสรจากแตนเพศเมีย จะให้ผลผลิตแตนรุ่นลูกมากกว่าช่อดอกที่ไม่ได้รับการผสมถึงสองเท่า ในขณะที่เมื่อแตนเพศเมียเก็บละอองเกสรไปผสมแต่ไม่สามารถวางไข่ได้พบว่าช่อดอกทั้งหมดหลุดร่วงไป อาจกล่าวได้ว่ามะเดื่อเพศผู้ต้องการพฤติกรรมการวางไข่จากแตนเพศเมีย เพื่อกระตุ้นการพัฒนาของดอกกอล หรืออาจเนื่องจากพฤติกรรมของแตนเพศเมียที่ไม่ยอมผสมเกสรให้มะเดื่อหากแตนไม่สามารถวางไข่ได้

TABLE OF CONTENT

TABLE OF CONTENT (CONTINUED)

TABLE OF CONTENT (CONTINUED)

LIST OF TABLES

LIST OF TABLES (CONTINUED)

LIST OF FIGURES

LIST OF FIGURES (CONTINUED)

LIST OF FIGURES (CONTINUED)

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CHAPTER I

INTRODUCTION

1. 1 PRINCIPLE AND RATIONALE

Climate change and global warming are the recently critical problems of the world. They affect the environment, global vegetation, seasonal periods and also all of ecological relationships. The effects are still increasing. Tropical forests are regarded as one of the most important ecosystems that provide resources and release a huge amount of oxygen. Therefore, biodiversity and ecology knowledge in the tropic areas are still necessary to be investigated and preserved.

Not many plant species are regarded to be 'key stone' of the forests, *Ficus* or fig trees are one of these in tropical forests (Power, 1966 in Shanahan *et al.*, 2001a; Benders, 2002). It is one of the large genera that contains about 750-1,000 species worldwide; about 120 species in North and South America, 105 species in Africa, approximate 367 species in Asia and Australian regions. The remainders are probably in several areas, which are still undiscovered (Corner, 1965; Berg, 1989; Berg and Corner, 2005, Figure 1.1). In ecosystems, the fig fruits are year-round food supply for several animals such as pigeons, parrots, hornbills, toucans, monkeys, gibbons and fruit-eating bats. This genus is also a pioneer species of the forests because they are fast growing and widely distributed (Benders, 2002). In open areas, for example, landslips at altitude up to 1,500 m in Borneo, figs in section *Sycomorus* role good secondary vegetation. Although in Volcano Island, these plants can form their colonies e.g. the Krakatau Islands between Java and Sumatra and Long Island near Papua New Guinea (Shanahan *et al.* 2001b).

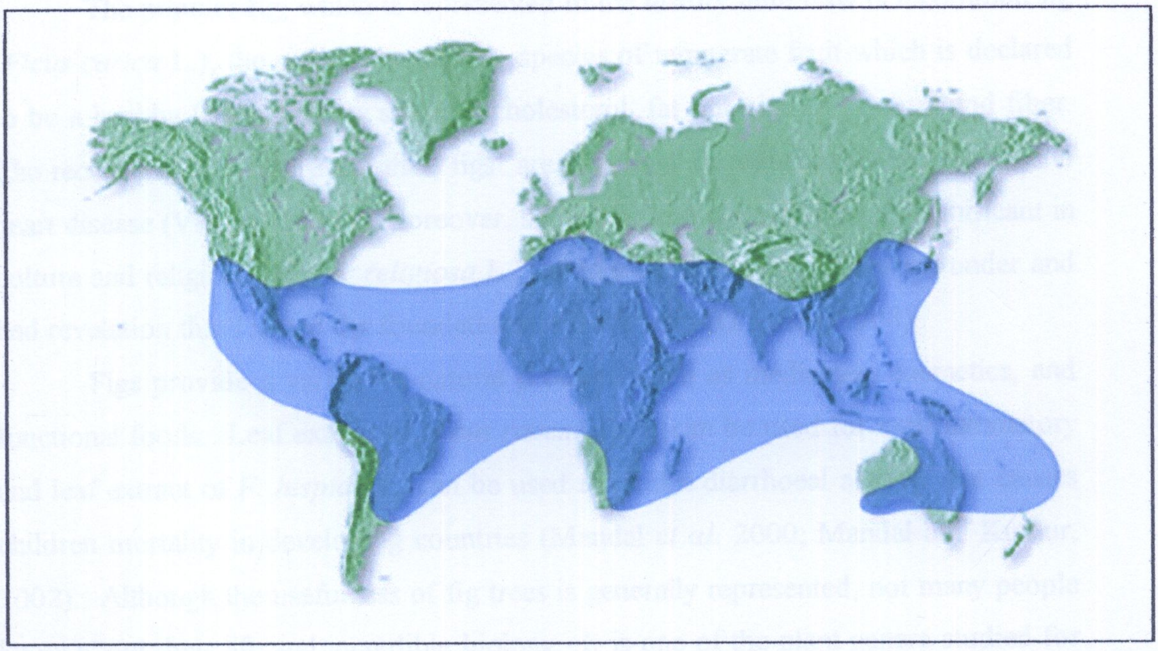


Figure 1.1 Distribution of *Ficus* species in the tropic zone (Noort and Rasplus, 2005a).

Figs are not only valuable for wild animals, but also for human as well. Condit (1969) reported that all parts of fig could be used, e.g. juvenile shoots and leaves of *F. virens* Aiton and *F. hirta* Vahl used as vegetable, ripe fruit of *F. nota* was sweet in taste. Latex of *F. benjamina* L. was used for inhibiting distribution of malaria mosquitoes, latex of *F. variegata* Blume, in Malaysia, used for Godang wax in batic dye and latex of *F. dusenii* used for bird's trapping. Some species were used for fiber and raw material for paper making. *Ficus carica* L. is a popular edible fruit and many species are used for gardening.

The fig is one of the earliest fruits cultivated; people use both fresh and dry figs to be the source of energy. It was included in many stories and history for a long time. 'Figs' frequently occurred in the bible and also included in the Eden Garden. The fig was the favorite fruit of Cleopatra and her death was caused by the asp (vipers snake) in the fig's basket. It was believed to be the best food for fast healthy recovering from sickness and make people look younger with a few wrinkles. In addition it was a highly prized in the original Olympic Games that the winners were given fig wreaths and fig as the price (Vinson, 1999).

The popular fig, which is represented in the history until now is a common fig (*Ficus carica* L.), the well-known edible species of temperate fruit which is declared to be a healthy fruit with low sodium, cholesterol, fat but high in calcium and fiber. The recent publications reveal that 'figs' are beneficial in reducing risk of cancer and heart disease (Vinson, 1999). Moreover, some of *Ficus* species are very significant in culture and religion; Bho, *F. religiosa* L., the tree that the lord Buddha sat under and had revelation that formed the foundations of Buddhism (O' Brien, 2008).

Figs provide a variety of natural products such as medicines, cosmetics, and functional foods. Leaf extract of *Ficus racemosa* L. can be used for anti-flammatory and leaf extract of *F. hispida* L. can be used to inhibit diarrhoeal activity that causes children mortality in developing countries (Mandal *et al.* 2000; Mandal and Kumur, 2002). Although the usefulness of fig trees is generally represented, not many people know about their life and incredible biology. It is one of the plant genera studied for plant and animal evolution.

Each fig species is believed to have a unique pollinator and their interaction is thought to be one-to-one (one species of fig tree and one species of pollinator wasp). Their pollinators are the insects of Agaonidae family in order Hymenoptera. The interaction is called obligatory mutualism (Weiblen, 2002). The specific relationship is popular for biologists studying co-evolution between the two species. Although there are many studies of their relationship, it is rarely clear. To support the knowledge, their function and structure must be repeated in investigation, especially with the large number of species of the diverse genus. It will be beneficial to predict their crops and production, which related to other biotic components in ecosystem (Berg, 1989).

The knowledge and studies of this genus were conducted in some areas of the tropic zone, such as Africa, South America, Australia, India, Malaysia and South of China (Aigoin and Kjellberg, 2006). It was treated not only for pollination, but also other fields such as phenology, dispersal, distribution, germination, hybridization and phytochemistry.

In Thailand, it was expected approximately 80-100 species of figs distributed throughout, but there have been only a few research of these plants. Most of them were related to plant diversity in some areas or the usage of them. For example, the studies of ethnobotany in some areas of Thailand. Those publications reported the benefits of fig tree with indigenous knowledge such as the usage of juvenile leaves and syconium of *F. racemosa, F. auriculata* Lour., *F. lacor* Ham. and *F. fistulosa* Reinw ex. Bl. as vegetable. *F. racemosa, F. auriculata, F. semicordata* Buch-Ham. ex. J. E. Sm. and *F. hirta* Vahl were used as the fruits with sweet taste. Some species used as medicinal plants such as *F. hispida* (Ponpim, 1996; Tovaranonte, 1998, Tangtrakul *et al.*, 2001).

The knowledge of taxonomic study was just recently presented in a few years, however this genus is being studied taxonomically by the professional botanists of the Flora of Thailand Project (Berg, 2007). Unfortunately, the investigation of figs and their pollinators in Thailand have never been published. This information is very important as much as its taxonomy, because of their variation which is evolved by fig characters and their specific wasps for several millions of years. Chiang Mai has a diverse physical characteristics with the elevation from 310-2,565 m asl., many types of forest are represented such as dry evergreen forest, mixed deciduous forest, deciduous dipterocarp forest, lower montane coniferous forest (Santisuk, 2007). Therefore, it is a suitable site to study plant diversity and also this was chosen to investigate *Ficus* under the differences of microclimate and elevation.

1.2 OBJECTIVES

1. To study taxonomy of some figs and their pollinators
2. To investigate interaction between some figs and their pollinators

CHAPTER II

LITERATURE REVIEW

2.1 GENERAL INFORMATION OF CHIANG MAI

2.1.1 Location

Chiang Mai, the second largest city in Thailand, is located in the North of the country at latitude 17° 15′ N - 20° 16′ N and longitude 98° 03′ E - 99° 33′ E. Its altitude range is from 310 - 2,565 m asl. The area is covered by both heavily mountainous and valley areas and approximate 20,027 square kilometers with twenty two districts. The North is contacted to Myanmar, the East is contacted to Lamphun, Lampang and Chiang Rai provinces, the West is contacted to Mae Hong Son provinces and the South is contacted to Lamphun and Tak provinces (Figure 2.1).

2.1.2 Topography

A large part of the land is covered by mountains, which generally run from north to south pattern. The Thanontongchai mountain lies on the West and Phipannum and Khuntan on the East. The forests have several characters that mainly divided to highland and lowland. For example, dry evergreen forest and pine and oak forest are represented in the highland while mixed deciduous forest and dry dipterocarp forests are represented in the lowland (Graham and Round, 1994).

The highlands of Chiang Mai are very important because they are the places, which give birth to several streams and rivers. The largest and most important river of the city is 'Ping River', which is originated in the mountain of Chiang Dao, a unique limestone habitat for several endemic species. The highest mountain in Chiang Mai is Doi Inthanon and also the Kingdom's highest elevation (2,565 m asl). The residential areas are mainly in plain and basin, which are generally suitable for agriculture and farming. Main crops are rice, soybean, corn, vegetables and fruit plants.

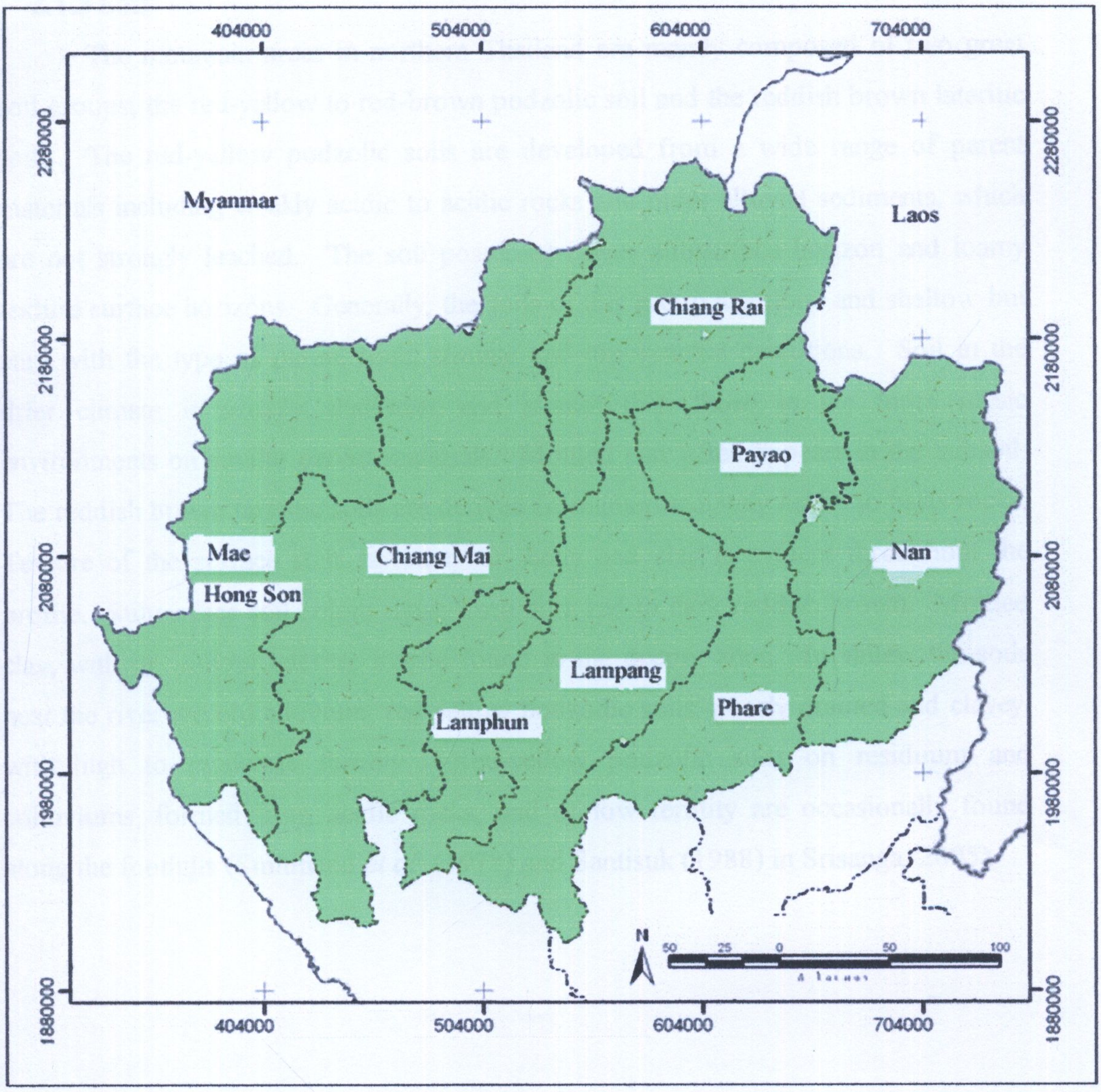


Figure 2.1 Map of Northern Thailand (Department of Geography, Faculty of Social Sciences, Chiang Mai University, 2007)

There are many minority people living in highland and generally produce vegetable and some of temperate plants (Graham and Round, 1994) (Figure 2.2).

2.1.3 Soil

The mountain areas in northern Thailand are mainly composed of two great soil groups; the red-yellow to red-brown podzolic soil and the reddish brown lateritic soils. The red-yellow podzolic soils are developed from a wide range of parent materials including weakly acidic to acidic rocks and older alluvial sediments, which are not strongly leached. The soil possesses clayey subsurface horizon and loamy texture surface horizons. Generally, the soils of this group are stony and shallow but vary with the type of parent rock, climate and topographic conditions. Soil in the drier climate is usually shallower and stonier than those in the more mesic environments on similar parent materials. Mottled clay often appears in the subsoil. The reddish brown lateritic soils are derived from intermediately acidic to basis rocks. Texture of the surface soils is loamy or sandy and clay is evident throughout the profile. Subsurface soil colors range from dark red to dark reddish brown. Mottled clay, with or without laterite, maybe found in the deeper zone. In valley, the soils near the river are old alluvium, red-yellow podzodic soils, poorly drained and clayey, with high to moderate fertility. Red-yellow podzolic soils on residuum and colluviums, formed from acidic rocks, and of low fertility are occasionally found along the foothills (Smitinand *et al.* (1978) and Santisuk (1988) in Srisanga, 2005)

Figure 2.2 Map of geography and topology of Chiang Mai (www.googleearth.com, 6 July 2007).

2.1.4 Climate

Chiang Mai is located in the monsoon zone, which is influenced mainly by two monsoons, firstly; southwest and northwest and secondly; cyclonic storms and intertropical fronts, which are typical of the climate of northern Thailand.

Three kinds of season occur in Chiang Mai composing of:

1) Cold and dry season (winter); during November to February, temperature is a bit cold in the winter averaging 13-15 ° C (Figure 2.3) and colder in the hills, sometimes as low as 0 ° C on the highland.

2) Hot and dry season (hot); during mid of February to mid May, temperature rises to 36-40 ° C (Figure 2.3) and is highest in April with low relative humidity of approximately 58-60 % (Figure 2.4).

3) Rainy season; during June to October, the rain generally falls sporadically (Figure 2.5) except during August and September when the streets of Chiang Mai can sometimes be flooded. The monsoon in this province begins in May and ends in October.

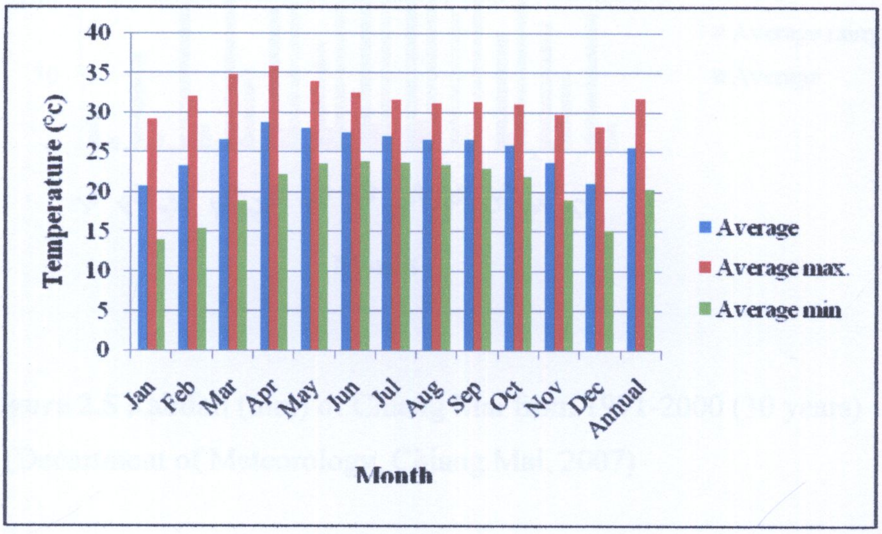


Figure 2.3 Temperature (°C) of Chiang Mai from 1971-2000 (30 years) (Department of Meteorology, Chiang Mai, 2007)

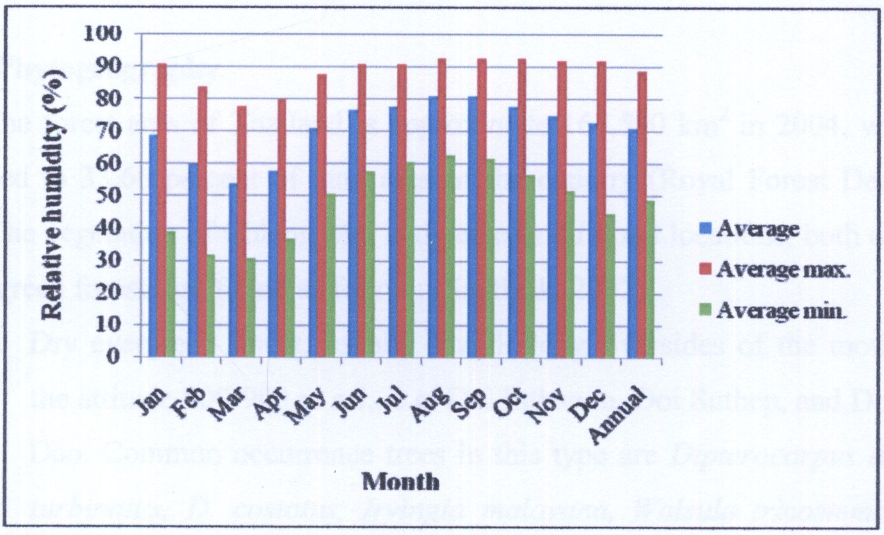


Figure 2.4 Relative humidity (%) of Chiang Mai from 1971-2000 (30 years) (Department of Meteorology, Chiang Mai, 2007)

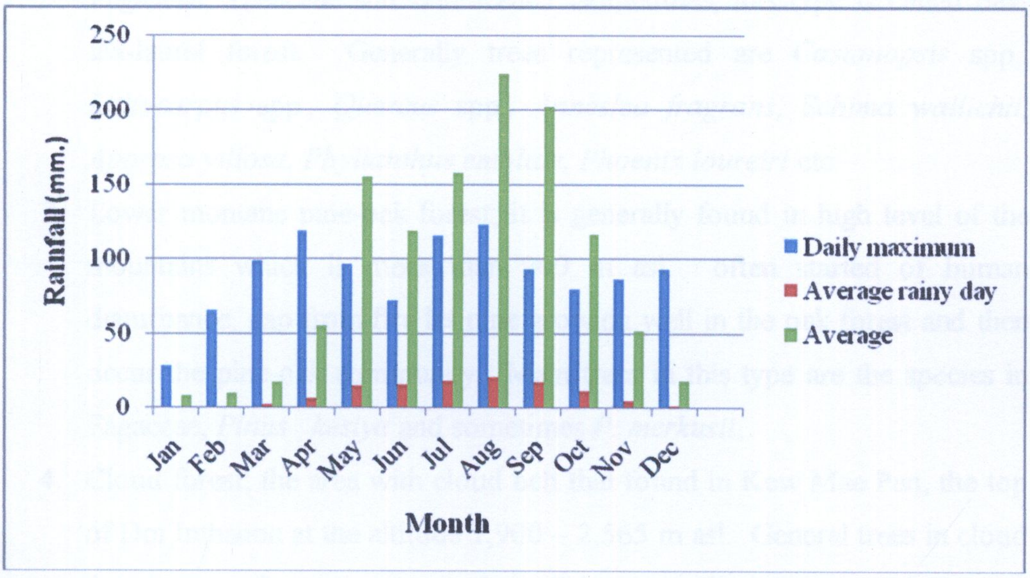


Figure 2.5 Rainfall (mm) of Chiang Mai from 1971-2000 (30 years) (Department of Meteorology, Chiang Mai, 2007)

In the period of 30 years from 1971-2000, the average rainfall was about 1,134 millimeter per annual, the average humidity was 71 % and the mean of temperature was 25.6 ° C (Department of Meteorology, Chiang Mai, 2007).

2.1.5 Phytogeography

The forest area of Thailand is approximate 167,590 km^2 in 2004, which was diminished to 33.66 percent of land area of the country (Royal Forest Department, 2008). The vegetation of Chiang Mai is diverse in different locations, both deciduous and evergreen forests are found as follow; (Santisuk, 2007)

1. Dry evergreen forest; usually found along riversides of the mountains at the attitude 800-900 m asl., e.g. Doi Inthanon, Doi Suthep, and Doi Chiang Dao. Common occurrence trees in this type are *Dipterocarpus alatus, D. turbinatus, D. costatus, Irvingia malayana, Walsula tricostemon, Ficus racemosa, Saraca indica, Cinnamomum* spp., *Mitrephora* spp. etc.
2. Lower montane oak forest; it is generally found in high level of the mountains, which is more than 900 m asl. They are mostly secondary forests after shifting cultivation. Main trees in this forest type are in

Fagaceae, Theaceae and Lauraceae. Sometimes, this type is called oak-tea-laurel forest. Generally trees represented are *Castanopsis* spp., *Lithocarpus* spp., *Quercus* spp., *Anneslea fragrans, Schima wallichii, Aporosa villosa, Phyllanthus emblica, Phoenix loureiri* etc.

3. Lower montane pine-oak forest; it is generally found in high level of the mountains which is more than 900 m asl. often started of human disturbance, gap from fire let pine growing well in the oak forest and then occur the pine-oak community. Main trees in this type are the species in Fagaceae, *Pinus kesiya* and sometimes *P. merkusii*.
4. Cloud forest; the area with cloud belt that found in Kew Mae Pan, the top of Doi Inthanon at the altitude 1,900 – 2,565 m asl. General trees in cloud forest are *Quercus eumorpha, Schima wallichii, Acer laurinum, Macropanax dispermus, Rhododendron arboreum*. Frequently occured epiphyte are *Agapetes hosseana, Rhododendron veitchianum, Neohymenopogon parasiticus* etc.
5. Upper montane scrub; the specific plant community that occurs in open areas on the top of limestone mountain, Doi Chiang Dao, at altitude 1,900-2,200 m asl. Main vegetation are small shrub and herbs growing in the crack of limestone. The dominant tree is *Trachycarpus oreophilus* (Palmae) with 3-10 m in height. General plants are temperate species and many of them are endemic species of Thailand. Some endemic species are *Luculia gratissima* var. *glabra, Viburnum atrocyaneum, Rhododendron ludwigianum, Primula siamensis*.
6. Mixed deciduous forest; it is generally represented in Chiang Mai and other places in the North of Thailand. The main plants are species in Leguminosae, Combretaceae, Verbenaceae, for example, *Afzelia xylocarpa, Butea monosperma, Cassia fistula, Pterocarpus macrocarpus, Terminalia chebula, Careya sphaerica, Suregada multiflora* etc.
7. Dry dipterocarp forest; its character is arid area with low nutrients and fire in hot season. Dominant species in this type are the species in Dipterocarpaceae such as *Dipterocarpus tuberculatus, D. obtusifolius, Shorea siamensis, S. obtusa*. Other plant species are *Gardenia*

sootepensis, Haldina cordifolia, Morinda pubescence, Xylia xylocarpa var. *kerrii, Parinari anamense, Aporosa villosa, Milientha suavis* etc.

8. Pine-deciduous dipterocarp forest; it is composed of Dipterocarp species and two pine species. Some species occurred in this type are *Pinus kesiya, P. merkusii, Dipterocarpus tuberculatus, D. obtusifolius, Shorea siamensis and S. obtusa, Aporosa villosa, Wendlandia tinctoria, Bauhinia variegata, Styrax benzoides* etc.

2.2 *FICUS* L. STUDIES IN THAILAND

Phromthep (1985) reported and described 18 species of *Ficus* in the survey of cauliflorous plants in some areas of Chiang Mai and Sakol Nakorn. Seventeen species were found in Chiang Mai and 11 species in Sakol Nakorn.

The common fig (*F. carica* L.) was introduced in highland cultivated area in 1986. It was addressed on morphology, anatomy and growth of two cultivars of this species (Nilsamranjit, 1986).

Phengklai (1996) surveyed plant diversity of Doi Inthanon National Park, it was found that three types of vegetation distributed under the factor of elevation. It was composed of dry-dipterocarp, moist deciduous and hill evergreen forests. There was about 1,274 plant species identified, but only a fig, *Ficus virens*, reported.

Gardner *et al.* (2000) reported that the genus *Ficus* consisted of the large number of species distributed in Northern Thailand. They mainly disperse from altitude 300-1200 m, but rarely in highland. There are commonly found in moderate to moist areas near rivers or streams.

Chantarasuwan and Charernsuk (2007) found that there were about 50 fig species distributed in Khao Nan National Park, Nakhon Sri Thammarat Province. The couple of well known species conserved were *F. fistulosa* Reinw. ex Blume and *F. obpyramidata* King. Another research in the same site study was an observation of frugivores on dried fig (*F. tinctoria* Forst.f. subsp. *gibbosa* (Blume) Corner). It was implied that 17 species of birds and one species of squirrel feed on this (Rakkien *et al.*, 2007).

In Northeastern Thailand, a taxonomic revision of the genus *Ficus* was recognized that there were about 44 species from the 6 subgenera in the region (Tanming and Chantaranothai, 2007).

Berg (2007), who studied figs of Thailand, found that at least twenty species of *Ficus* have more or less problematic description and need to be discussed such as *Ficus anstomosans* Wall. ex Kurz, *F. anserina* (Corner) C.C Berg, *F. auriculata* Lour., *F. griffithii* (Miq.) Miq., *F. geniculata* Kurz etc.

2.3 CLASSIFICATION OF *FICUS*

There are about 1,000 species of *Ficus* distributing in tropic and sub-tropic regions of Asia, Australia, mid and south America and South-Africa. Especially, they are highly diverse in Southeast-Asia (Zhekun and Gilert, 2003). In Thailand, approximate 80-100 species are distributed in deciduous, dry evergreen and evergreen forests (Smitinand, 2001).

Ficus is a member of Moraceae or jackfruit's family. Its habits are diverse such as trees, shrubs, climbers or stranglers with latex. They are both evergreen and deciduous as monoecious and dioecious species. For monoecious species, they consist of male, gall (sterile female) and female flowers in each special inflorescence 'syconium' (sykos in Greek means fig; Kjellberg *et al*, 2005). For dioecious species, they consist of male and female trees. Syconium of male trees composes of male and gall flowers but inside the syconium of female trees, only female flowers are found (Zhekun and Gilert, 2003).

In the history of classification, Berg and Corner (2005) said that the first simple subdivision of *Ficus* designed by Thunberg in 1786 and adapted by Vahl in 1805 was based on the leaf shape. In 1867, Miquel separated these plants into a genus (with 472 species) and then King revised by adding two new sections, *Palaeomorphe* and *Neomorphe*, but retained most of Miquel's subgenera and sections in 1887-1888. During 1960-1965, Corner followed Miquel's work on floral construction and added more details of fruit's character and anatomy. His work, manuscript of *Ficus*, was published more than 30 years ago.

The important characteristics for distinguishing *Ficus* to subgenera as Berg (2003a) described are;

1. Monoecy-dioecy

Naturally, *Ficus* spp. represent both monoecious and dioecious, the monoecious fig (syconium) comprising of staminate (male) flowers and pistillate (female) flowers with different style-lengths. Short and long style scattered inside the fig and all female flowers can produce seeds. Hence, a syconium of monoecious figs can produce both wasp and seeds. In dioecious fig, they are two types of plants composing of male and female trees. In male tree syconium, there are staminate flowers and short-styled flowers (gall flowers), in which the first group arranges near the ostiole. This kind of plant produces only wasps offspring, sometimes call 'gall figs'. The other is female tree, in which a syconium of them can produce only seeds from the long-styled flowers called 'seed figs'.

2. Adventitious roots

The characteristic of producing adventitious roots basically represented in the growth form of hemi-epiphyte or in some types of climber. This type is evident in subgenus *Urostigma* which produces a large system to support the main trunk (banyan). However, in other groups, the adventitious roots are not showy. Some form aerial roots for climbing stem and some for creeping stem.

3. Stipules

Mostly, fully amplexicaul stipule is represented and usually leaving annular scar in this genus. Lateral or semi-amplicaul stipule occurs in subgenus *Sycidium* and subgenus *Ficus*.

4. Position of figs

Figs mostly are born in the leaf axils in either pair or solitary. Sometimes they are found below the leaves, especially if the tree growth is rhythmic. Many fig species are ramiflorous that means figs were born in the old wood. Cauliflory also occurs in most subgenus but frequently in subgenus *Sycidium* and *Sycomorus*. Another character is fig-bearing on the base of trunk or stolon-like called geocarpy or flagellifory such as *F. semicordata* and *F. hispida* in subgenus *Sycomorus*.

5. Bracts

In *Ficus*, there are many kinds of bracts demonstrated and it is one of the most important features to classify. At least seven types are distinguished in Berg (2003) (Table 2.1).

6. Waxy glands

Most species of *Ficus* present waxy glands, with small glandular spots and waxy surface. In *Urostigma*, a single gland occurs on the base of the midrib. All other genera, waxy glands are found in the axil of the basal lateral veins. In *Sycomorus* section *Sycocarpus*, they present in the axil lateral veins in the middle of the lamina. Some groups of fig are lacking of waxy glands such as subgenus *Pharmacosycea* and some species of subgenus *Ficus* and subgenus *Sycomorus*.

For the Asian-Australasian region, *Ficus* is divided to three subgenera of monoecious, *Pharmacosycea* (two sections world-wide; *Oreosycea* and *Pharmacosycea*), *Sycomorus*, and *Urostigma* (with 7 sections world-wide; *Americana, Conosycea, Galoglychia, Leucogyne, Malvanthera, Stilpnophyllum* and *Urostigma*) and a group of dioecious species in subgenus *Ficus*. The latter consists of 8 sections; *Adenosperma, Ficus, Kalosyce, Neomorphe, Rhizocladus, Sinosycidium, Sycidium* and *Sycocarpus* (Berg and Corner, 2005). In 1986, Berg proposed the subdivision of the African section *Galoglychia* into 6 subsections. After that he modified the knowledge in 2003 by emphasizing more and vegetative characters and divided to six subgenera (Zhekun and Gilert, 2003; Berg, 2003a; Berg and Corner, 2005).

Table 2.1 Types and characters of bracts in *Ficus* (Berg, 2003a)

No.	Bract Type	Characters
1	Subtending bracts	Either small or large size. In subgenus *Sycidium* frequently small and inconspicuous, but in subsection *Malvanthera* is small to large and fuse. Sometimes subtending bracts forming a calyptrate structure enclosing young figs, which represent in subgenus *Urostigma.*
2	Peduncular	There are at least three or four bracts scattered on the peduncle. These usually found in subgenus *Sycidium* and sometimes in subgenus *Pharmacosycea* (section *Oreosycea)* and subgenus *Sycomorus* (section *Adenosperma).*
3	Basal	These characters can be found all of subgenus with two or three whorl arranged at the base of receptacle.
4	Lateral	Few or numerous bracts occur an outer surface of receptacle few. They are usually found in subgenus *Sycidium* and *Sycomorus* and occasionally in subgenus *Pharmacosycea.*
5	Apical	Bracts arranged around the ostiole.
6	Ostiolar	These usually numerous bracts arranged in the ostiole. The pattern of arrangement varies in different groups. In most subgenera, there are three or two horizontal, more or less semicircular and imbricate bracts closing the entrance. In subgenus *Urostigma* section *Galoglychia,* these bracts are tightly packed and make the narrow entrance. But in *Sycidium,* the ostiolar bracts are more loosely-interlocking (Berg and Wiebes, 1992; Berg, 2003a).

Table 2.1 Types and characters of bracts in *Ficus* (Berg, 2003a) (continued)

No.	Bract Type	Characters
7	Interfloral	These bracts are born among the flowers, sometimes on the pedicels. They are found in subgenus *Pharmacosycea, Urostigma* and *Sycomorus* and may absent in all other subgenera. In subgenus *Urostigma*, sometimes the interflora bract lack and likely internal hair.

The characteristics of six subgenera are described by Berg (2003a) as follow;

Subgenus *Pharmacosycea* (Miq.) Miq.;

Terrestrial trees or shrubs without adventitious roots, monoecious. Leaves usually spirals; lamina symmetric, mostly coriaceous, the margin mostly entire; waxy mostly in the axils of the basal lateral vein beneath, sometimes absent; stipules fully amplexicaul. Fig axillary, sometimes just below the leaves, rarely cauliflorous; basal bracts 3, verticillate; lateral bracts absent, occasionally present; ostiole with interlocking bracts, few upper ones visible; interfloral bracts usually present; internal hairs mostly absent. Staminate flowers scattered among the pistillate ones; stamens 1 or 2; pistillode sometimes present. Stigmas usually 2, subulate and not conspicuously papillate. Fruits achenes.

These plants distribute from Africa to Australia and the Pacific and in tropical America; ca. 80 species such as *F. callosa* Willd., *F. nervosa* Heyne ex Roth, *F. vasculosa* Wall. ex Miq., etc.

. The specific species of pollinator wasps are mainly in *Dolichoris* (sect. *Oreosycea*) and *Tetrapus* (sect. *Pharmacosycea*).

Subgenus *Urostigma* (Gasp.) Miq.;

Hemi-epiphythic, hemi-epilithic, or less commonly terrestrial trees with aerial adventitious roots, which often replace the primary root-system, monoecious. Leaves mostly in spirals, sometimes subopposite; lamina symmetric, mostly coriaceous, the margin mostly entire; a single waxy gland at the base of the midrib beneath; stipules fully amplexicaul. Figs axillary or just below the leaves, sometimes ramiflorous or cauliflorous; basal bracts 2 or 3, verticillate; lateral bracts absent; ostiole with interlocking bracts and the ostiole circular with 2 or 3 bracts visible or the upper ostiolar bracts descending and the aperture slit-shaped or triradiate; interfloral bracts usually present; internal hairs (bristles) sometimes present. Staminate flowers scattered among the pistillate ones or sometimes near the ostiole; stamen 1 (or 2); pistillode usually absent. Stigmas mostly 1, sometimes 2, filiform, mostly conspicuously papillate. Fruits achenes or drupaceous.

These plants distribute from Africa to Australia and the Pacific, and in tropical America; ca. 280 species such as *F. bengalensis* L., *F. elastica* Roxb., *F. religiosa* L., etc.

This subgenus is mainly pollinated by species of *Agaon, Alfonsiella, Allotriozoon, Courtella, Deilagaon, Elisabethiella, Eupristina* (subgenus *Eupristina and Parapristina*), *Nigriella, Paragaon, Pegoscapus, Platyscapa, Pleistodontes, Watersoniella,* largely associated with entities at the section or subsection level (Wiebes, 1994).

Subgenus *Ficus* Corner;

Terrestrial trees or shrubs, rarely holo-epiphytic, with adventitious roots only on creeping stems, dioecious. Leaves in spirals; lamina symmetric, often subcoriaceous to chartaceous, the margin often dentate (or lobate); waxy glands mostly in the axils of the basal lateral veins beneath, also (or only) in furcations or on the nodes of leafy twigs; stipules fully amplexicaul, sometimes semi-amplexicaul. Figs in the leaf axils or just below the leaves; basal bracts 3, verticillate; ostiole relatively large, mostly with more than 3 upper ostiolar bracts visible; internal bracts absent; internal bristles mostly present. Tepals often hairy. Staminate flowers near the ostiole or scattered among the pistillate ones; stamen 1-3 (-4); pistillode usually absent. Stigmas of long-styled flowers often 2, subulate, without conspicuous papillae. Fruit achene.

Distribution is from eastern Malesia to north-eastern Africa and the Mediteranean; ca. 60 species such as *F. carica* L., *F. hirta* Vahl, *F. pandulata* Hance, etc. This subgenus is mainly pollinated by *Blastophaga* and *Valisia*.

Subgenus *Synoecia* (Miq.) Miq.;

Root-climbers with short adventitious root on climbing stems, dioecious. Leaves distichous, rarely in lax spirals, those of the climbing stems and branches (acrophylls) different from those of the non-climbing (and fertile) branches (acrophylls); lamina symmetric (acrophylls) or asymmetric (bathyphylls), coriaceous (acrophylls) or sub-coriaceous to chartaceous (bathphylls), the margin entire; waxy glands in the axils of the basal lateral veins beneath, rarely on the nodes of leafy twigs. Figs axillary or just below the leaves, sometimes ramiflorous or cauliflorous; basal bracts 3, verticillate; interfloral bracts absent; ostiole relatively small, with few (3) upper ostiolar bracts visible; internal hairs mostly present. Tepals glabrous (rarely hairly). Staminate flowers near the ostiole or scattered among the pistillate ones; staminate 1 or 2 (or 3); pistillode usually absent. Stigmas of long-styled flowers often 2; subulate. Fruits achenes.

These plants distribute from Solomon Islands and Australia to Japan and Sri Lanka; ca. 75 species such as *F. pumila* L., *F. laevis* Blume, *F. sarmentosa* Buch-Ham., etc. Pollinators of this group is *Wiebesia* (Wiebes, 1994).

Subgenus *Sycidium* (Miq.) Mildbr. & Burret;

Terrestrial shrubs or trees with adventitious roots only on creeping stems or climbers, creeping, hemi-epiphytes or subepiphytic with adventitious roots, dioecious. Leaves in spirals, distichous, subopposite or subverticillate; lamina often chartaceous to subcoriaceous, mostly asymmetric, the margin often dentate (to lobate); waxy glands on the lower surface of the lamina. In the axils both main basal lateral veins, or only in one of them, or sometimes a third in the axil of a lesser basal lateral vein, or sometimes both occur largely on the midrib and then occasionally fused, or sometimes (smaller) ones in the axils of other lateral veins; stipules semi-amplexicaul to lateral or less frequently fully amplexicaul. Figs in the leaf axils, just below the leaves, ramiflorous, cauliflorous, or sometimes flagelliflorous; peduncular bracts usually scattered on the peduncle; lateral bracts frequently present; interfloral bracts absent; ostiole usually with numerous upper bracts visible; internal hairs usually present. Staminate flowers near the ostiole; stamens 1 (or 2); pistillode (or pistil) always present. Stigma (also of long-styled flower) 1, truncate. Fruits achene or druplets.

This subgenus distribute from Africa to Australia and the Pacific; ca. 110 species such as *F. semicordata* Buch-Ham., *F. tinctoria* G. Forster, *F. heterophylla* L., etc. Their pollinators are the species of *Kradibia*; sect. *Sycidium* and *Liporrhopalum*; sect. *Paleomorphe* (Wiebes, 1994).

Subgenus *Sycomorus* (Gasp.) Miq.;

Terrestrial trees or shrubs, with adventitious roots only on creeping branches, large trees often buttressed, not epiphytic plants, dioecious or monoecious. Leaves in spirals, subopposite, or distichous; lamina symmetric or asymmetric, coriaceous or chartaceous to subcoriaceous, the margin often dentate; waxy gland in the axils of the basal lateral veins, also or only in the axils of the other lateral veins, often also in furcation of veins beneath, or also on the nodes of leafy twigs; stipules fully amplexicaul. Fig axillary, just below the leaves, ramiflorous, cauliflorous and/or flagelliflorous; basal bracts if distinct, then mostly 3 and mostly verticillate; interfloral bracts absent; ostiole often large with numerous upper bracts visible; internal hairs usually present. Staminate flowers near the ostiole, nearly always subtended by 2 bracteoles; stamens 2; pistillode usually absent. Stigma (also of long-styled flowers) 1, usually truncate. Fruits achenes.

These plants distribute from Africa to the Pacific; ca. 140 species such as *F. racemosa* L., *F. hispida* L., *F. auriculata* Lour., *F. fistulosa* Reinwardt ex Blume, etc. The pollinator is the species of *Ceratosolen* (subgenera *Ceratosolen, Rothropus and Strepitus)* (Wiebes, 1994).

Recent studies of classification were supported by relationship with their pollinator fig wasps. Most genera of figs and fig wasps are matched except a few cases in subgenus or section of *Ficus*. However, analyses based on molecular studied by Weiblen also supported this classification (Berg and Corner, 2005).

In Thailand, there are about 80 species of *Ficus* listed in Thai-plant name, a book of botanical name references, by Smitinand (2001). However the description of them is being processed. A record of plant collection in BKF showed that Corner had visited and studied some fig trees in Thailand during 1960s (Corner, 1965). Some figs are recently described in Thai forest bulletin by Cornelis C. Berg who is continuously working on Thai fig taxonomy.

2.4 CLASSIFICATION OF FIG WASPS

2.4.1 History of the study

The history of fig wasp studies were described by Wiebes (1994). The study of the Indo-Australian fig wasps was started in 1883 when Saunders and Westwood published their work of fig insect's description from India (Wiebes, 1994). Ceylon and Australia including two Indo-Australian Agaoninae species. Then, some researchers add some description of their work during the later past of the decade (Table 2.2).

Table 2.2 The genera of the Indo-Australian Agaoninae and the groups of their host-figs (after Wiebes, 1994)

AGAONINAE	***FICUS*** sub section	sub series
AGAONINI		
Pleistodontes	*Malavanthera*	
	Stilpnophyllum	
BLASTOPHAGINI		
Dolichoris	*Oreosycea*	
Platyscapa	*Urostigma*	
Delilagaon	*Conosycea*	Validae
Waterstoniella	*Conosycea*	Zygotricheae & Crassirameae
	Dictyoneuron	
E. (Eupristina)	*Conosycea*	Drupaceae & Indicae

Table 2.2 The genera of the Indo-Australian Agaoninae and the groups of their host-figs (after Wiebes, 1994) (continued)

AGAONINAE	***FICUS*** sub section	sub series
E. (Parapristina)	*Benjamina*	Benjaminaeae & Callophylleae
	Leucogyne	
B. (Blastophaga)	*Ficus*	
B. (Valisia)	*Eriosycea*	
Webesia	*Rhizocladus*	
	Kalosycea	
C. (Strepitus)	*Auriculisperma*	
	Dammaropsis	
	Papuasyce	

Bouček (1988) gave a useful description of fig wasp classification of the Australasian region that composed of Australia, Papua New Guinea and New Zealand.

2.4.2 Taxonomic studies

Fig wasp is a group of many kind of wasps living together with fig trees. They are mostly in family Agaonidae and Chalcididae, superfamily Chalcidoidae, Order Hymenoptera (Bouček, 1988).

Agaonidae family currently includes 76 genera and 757 species placed in 6 subfamilies (Pitkin, 2004). This family is generally known as fig insects or fig wasps until recent study. The group that functions as pollinator is placed in only a subfamily Agaoninae, whereas the others are probably parasitoids of the pollinators or gall-formers of other parts of figs (Figure 2.6) (Bouček, 1988; Pitkin, 2004).

The other groups of fig wasps are in the Chalcididae family. It includes 70 genera distributed worldwide, but a few occurrences in the cold region. The number of species reported in Australasia (Australia, Papua New Guinea and New Zealand) is about 176 species, but not known all over the world. All species develops as parasites on other pupae insects such as Lepidoptera, Coleoptera, Diptera, Neuroptera, and Hymenoptera (Bouček, 1988).

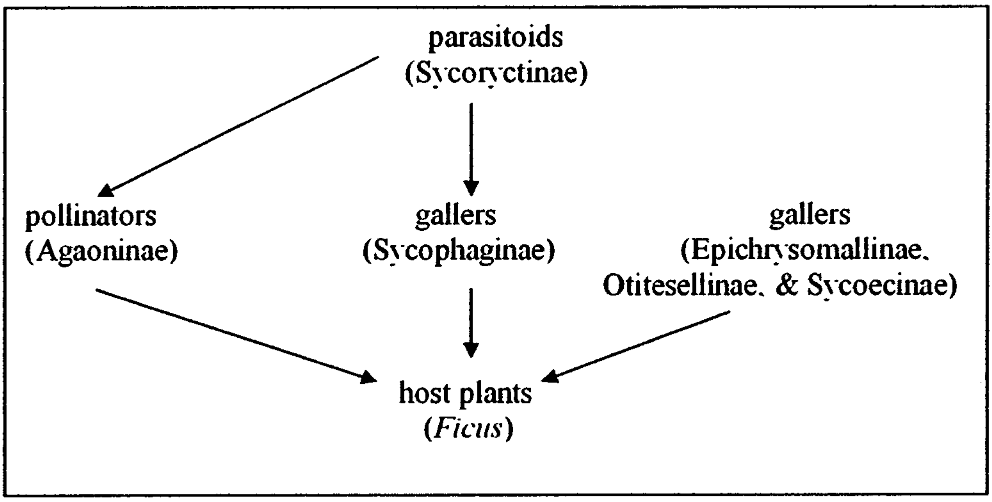


Figure 2.6 Trophic relationships among figs and fig wasps. Agaonid subfamilies include pollinators, gallers, and parasitoids (after Weiblen, 2002).

Fig's pollinators are only in the Agaonidae, especially in subfamily Agaoninae. Wiebes (1994) suggested separating this subfamily of fig wasps from the other groups. Some pollinator wasps of Agaoninae are *Pleistodontes, Eupristina, Ceratosolen, Liporrhopalum, Blastophaga*, etc. Some wasps are not pollinators, but living with figs by function parasitoid or gall – forming such as *Apocrypta* in subfamily Sycoryctinae, and *Apocryptophagus*, *Sycoscapter*, *Pilotrypesis* in subfamily Sycophaginae (Bouček, 1988).

2.4.3 The Agaoninae characters

Agaoninae is the most specific wasps with their fig trees, not only morphological succeed characters but also biological adaptation. Wasp offspring can not success in developing outside the syconium, as well as fig flowers can not produce seeds without pollination by its particular wasp (Ramirez 1970 in Bouček, 1988).

The morphological adaptation occurred in both male and female wasps. In female, their size is related to the ostiole of fig syconium. The fore and hind legs are short, strong and spiny in order to push the head forward when she enters to the ostiole (Figure 2.7). The mandibles are also strong with ventral laminae or row of denticle or fine teeth (Figure 2.8 a). The middle of the face has a broad channel or depression, which suits for the antennal scapes. The antennal scape is distinctly widened and the third segment is produced apically into a point (Figure 2.9).

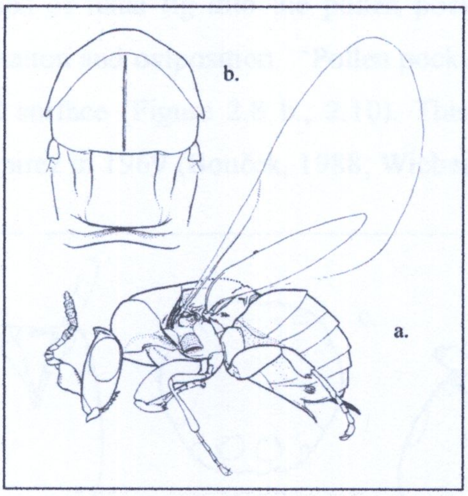


Figure 2.7 *Wiebesia partita*; *a.* female and *b.* thorax dorsum (after Bouček, 1988).

They entrance through the ostiole by teeth attach to the wall and then pull the head and body forward. The body will pass forward while the mandible pulls it with helping by the short, strong and spiny fore and hind legs. The wings are usually broad and strong for flying to another distant fig tree (Bouček, 1988; Berg and Wiebes, 1992; Wiebes, 1994).

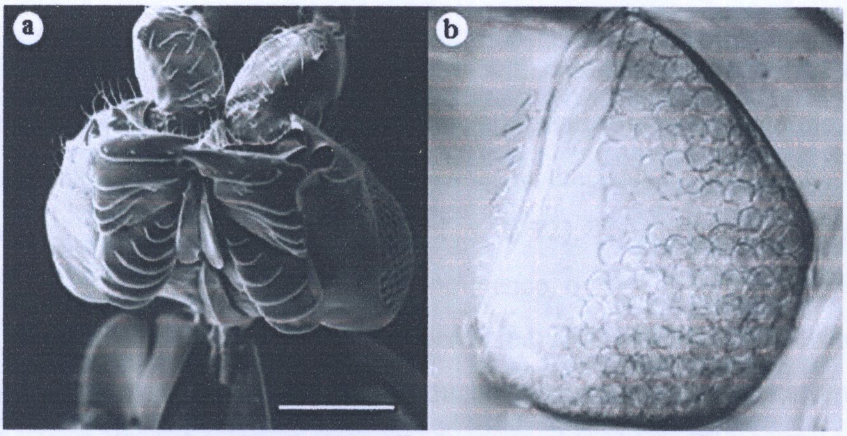


Figure 2.8 *a.* Ventral view of the female head of *Kradibia ohuensis* showing mandibular appendage with six lamellae (scale = 0.1 mm), *b.* Pollen pocket of *Ceratosolen kaironkensis* containing *Ficus microdictya* pollen grains (after Wieblen, 2002).

Another special female adaptation is 'pollen pocket' that occurred in most species of Agaoninae. In this character, female wasps intend to carry pollen grains to pollinate female flowers (Jousselin and Kjellberg, 2001; Kjellberg *et al.*, 2001). They collect lots of pollen grains of natal fig into the pollen pocket and fly to another receptive fig tree for pollination and oviposition. 'Pollen pockets' are flat pocket-like placed in the mesopleural surface (Figure 2.8 b., 2.10). This term was first called 'sternal corbiculae' by Ramirez in 1969 (Bouček, 1988; Wiebes, 1994).

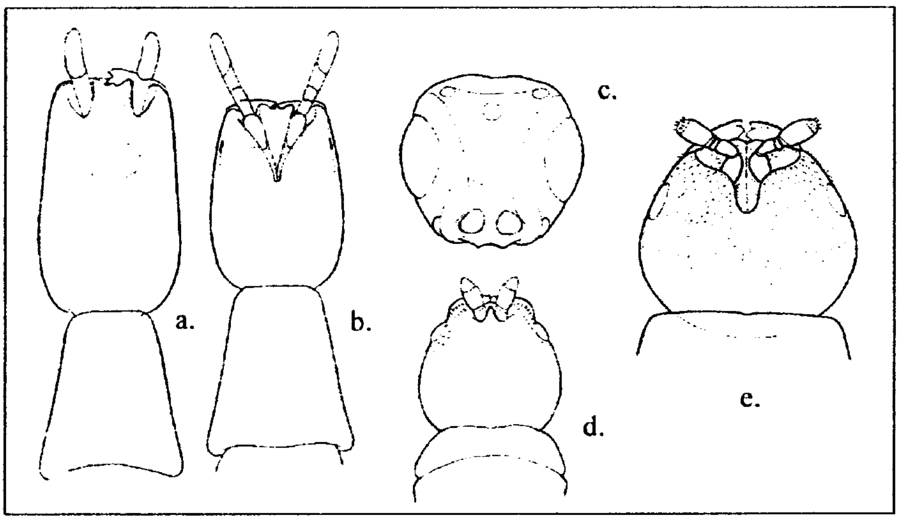


Figure 2.9 *a. Ceratosolen indigenus*; male head with pronotum, *b. C. vissali*; male head with pronotum, *c. Kradibia wassae*; female head, *d. Blastophaga vidua*; male head and *e. B. psense*; male head (after Bouček, 1988).

The males are smaller than the females with apterous, yellowish and small eyes or blind. The males also have strong fore and hind legs and mandible. Some groups of pollinators used for biting and opening in the wall of gall fruits, and for tunneling the wall of receptacle (Berg and Wiebes, 1992). The antennae are situated in separate grooves on either side of a medial prominence, or in a common groove in the frontal part of the head; the number of segments reduced. The legs have shortened spiny tibiae; the tarsal segments are often reduced in number. The gaster ends in a tube with the genitalia, often bearing small claspers with claws (Figure 2.10). The males emerge firstly into the cavity then bite a gall containing virgin female and mate them by telescoping to the female wasp gall. One male can mate more than one female wasp. Normally, the males do not leave the fig or just come out after mating and die in a few hours. Both male and female develop in the galled female florets of the fig (Bouček, 1988).

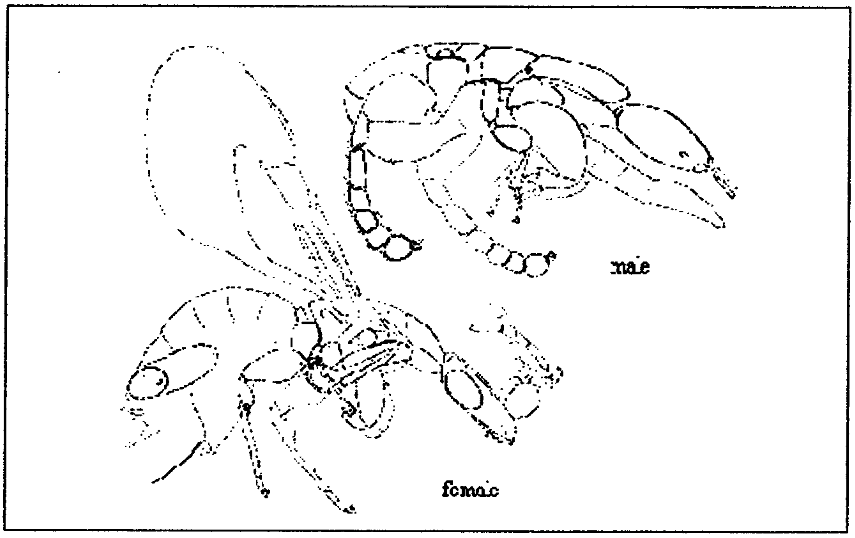


Figure 2.10 *Ceratosolen dentifer* Wiebes, female (left)-pollen pocket in the mesosternum of the thorax and male (right)-with the large hirsute hind legs (after Wiebes, 1979).

2.5 BIOLOGY OF FIG AND FIG WASPS

Figs and their pollinators were recorded as fossil beyond 90 million years ago (Machado *et al.*, 2001). The symbiosis figs and their pollinating wasps (Agaoninae) form is a typical co-evolution study. They cannot live and reproduce without each other. Although figs can grow individually, their seeds could not be produced without pollination. Also the pollinators can live only a few days outside the syconium (Berg and Wiebes, 1992).

2.5.1 The development of the Figs

The fig inflorescence is called "fig" or "syconium" with the fruit-like shape. This character is evolved from receptacle. Inside the syconium, lots of tiny flowers born on the inner side. Inside each syconium, it is composed of 50-7,000 unisexual flowers (Endress, 1994). In the development of the syconium, Galil and Eisikowitch (1968) distinguished to 5 phases (Figure 2.11).

Galil and Eisikowitch (1968) revealed the description of 5 phases of fig development as follow;

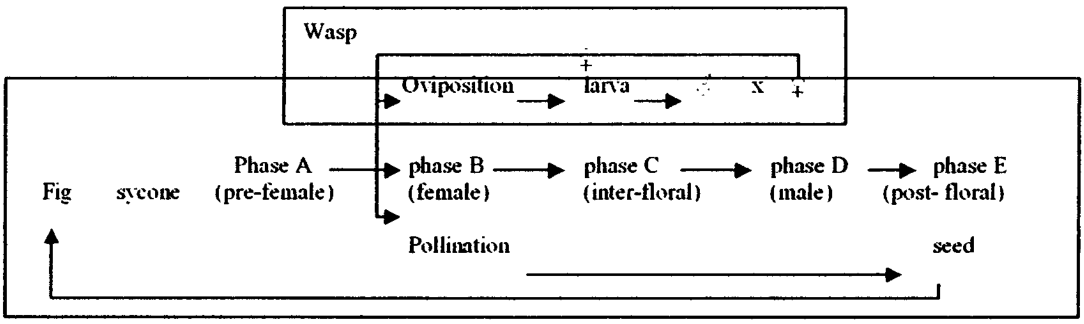
A. Pre-female phase, during which the inflorescence and the flowers develop until the receptiveness of the stigma of the pistillate flowers.

B. Female phase, in which the ovules become fully developed, the stigma are receptive, and the ostiole becomes penetrable for the pollinators as they enter to pollinate and oviposit.

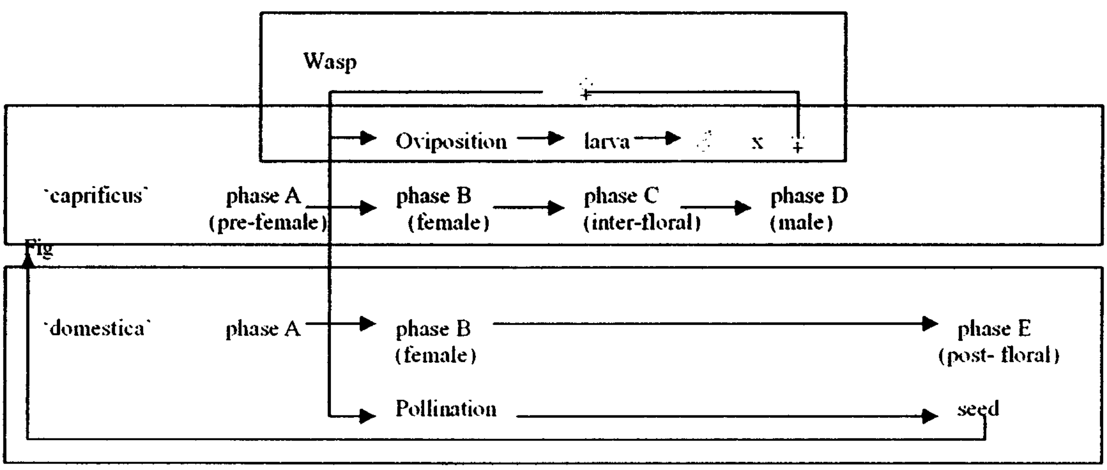
C. Interfloral phase, in which the larvae of the pollinators develop to immaturity and the fig-seeds develop to maturity. This phase separates the anthesis of the pistillate flowers from that of the staminate flowers.

D. Male phase, in which the insects emerge from their galls. The pollen was already mature in an earlier (i.e., the female) phase, but now it becomes exposed by the elongation of the filament and/or the opening of the thecae. The male pollinators mate with the females while they are still in their galls, then the females emerge, collect pollen and leave the syconium through the ostiole or via tunnels made by the males.

E. Post-floral phase, in which the fruitlets become mature and the syconium become soft and attractive to organisms that disperse the fruits.



a. monoecious fig



b. dioecious fig

Figure 2.11 Development phase of monoecious and dioecious figs; *a.* Generalized cycle of a monoecious figs and its pollinator wasp. The developmental phase of the syconium (A-E), *b.* Generalized cycle of a dioecious fig and its pollinator wasp. The female cycle (domestica-form of *Ficus carica*) run from phase A, over the pollinated flower in phase B, directly to the seeds of phase E; the male cycle (caprificus-form) from phase A, over the galled flower in phase B and the inter-floral phase C, to the male phase D from which the female and male emerge (after Wiebes, 1979).

Several characters of monoecious and dioecious figs are distinguished and those are very important to identify and useful for studying many issues of them. Berg and Wiebes (1992) demonstrated some features in Table 2.3.

Table 2.3 Some features of monoecious and (gyno) dioecious figs (after Berg and Wiebes, 1992).

Feature	Monoecious	Dioecious
Inflorescences with:	Staminate fl. > 40-48% Short-styled fl. 40-48% Long-styled fl. 3-10%	a. gall fig: staminate fl. 3-35% short-styled fl. 95-65% b. seed fig: long-styled fl. 100% or with neuter fl.
Heterostyly:	Imperfect	Perfect
Ovaries at anthesis:	not lined up	lined up
Ovules:	all can form seeds	a. short-styled fl.: do not usually form seeds b. long-styled fl.: all can form seeds
Flowering:	mostly (excl. *Sycomorus*) individuals synchronous populations asynchronous	a. gall fig trees: b. individuals often asynchronous, fig crops not separate or ± asynchronous b. seed fig trees: (probably) often synchronous with separate (seasonal?) fig crops

Table 2.3 Some features of monoecious and (gyno) dioecious figs (after Berg and Wiebes, 1992). (continued)

Feature	Monoecious	Dioecious
Represented in:	ca. 50% of the species in Old and New World: '*Pharmacosycea* group' '*Urostigma* group' '*Sycomorus* group'	ca.50% of the species in the world: '*Ficus* group' '*Sycidium* group' '*Sycomorus* group'

2.5.2 Habits and ecology

Distribution of *Ficus* is generally limited between the latitudes 35° N and S, but some can be found in the sub-temperate zone like *F. carica* growing in Europe and Asia Minor. In the tropic zone, it is distributed worldwide both in new and old world. Subgenus *Pharmacosycea* and *Urostigma* range in the old world from Pacific to West Africa and some in Neotropics. Subgenus *Sycidium* and subgenus *Sycomorus* range from the Pacific to west Africa, while subgenus *Ficus* and subgenus *Synoecia* are limited in only the Malesian region and Asian mainland (Berg. 2003b).

This genus shows diverse growth-forms both terrestrial shrubs and trees. Usually, habitats are comprised of hemi-epiphytes (many of them being potential 'stranglers' and some exhibiting the 'banyan'- habit), holo-epiphytes, climbers (among with a group of root climbers), creeping shrubs, rheophytic shrub, etc. (Berg and Corner, 2005). Their lives spans tend to vary from a few years in pioneer shrub to over 1000 years in the biggest banyans. The oldest tree known is *F. religiosa* L. that planted in Anuradhapura, Sri Lanka, by King Tissa in 288 BC. (Lewington and Parker, 1999 in Harrison, 2005).

About 50% of the fig-species are potentially hemi-epiphytic and about 50% have a terrestrial life-form. Hemi-epiphytism is usually represented in subgenus *Urostigma*. They start their life as epiphytes at some suitable areas on a host tree, such as in the bark, cracked or broken branches. It usually sends down a (tap) root along the trunk of the host. When it reaches the soil, it can access more nutrients to promote its growth. The root-system expands and may form a root-basket around the trunk of the host, and then hemi-epiphyte fig may kill the host-tree by the root-basket around the trunk (Figure 2.12). It is called 'strangling' (Berg and Wiebes, 1992).

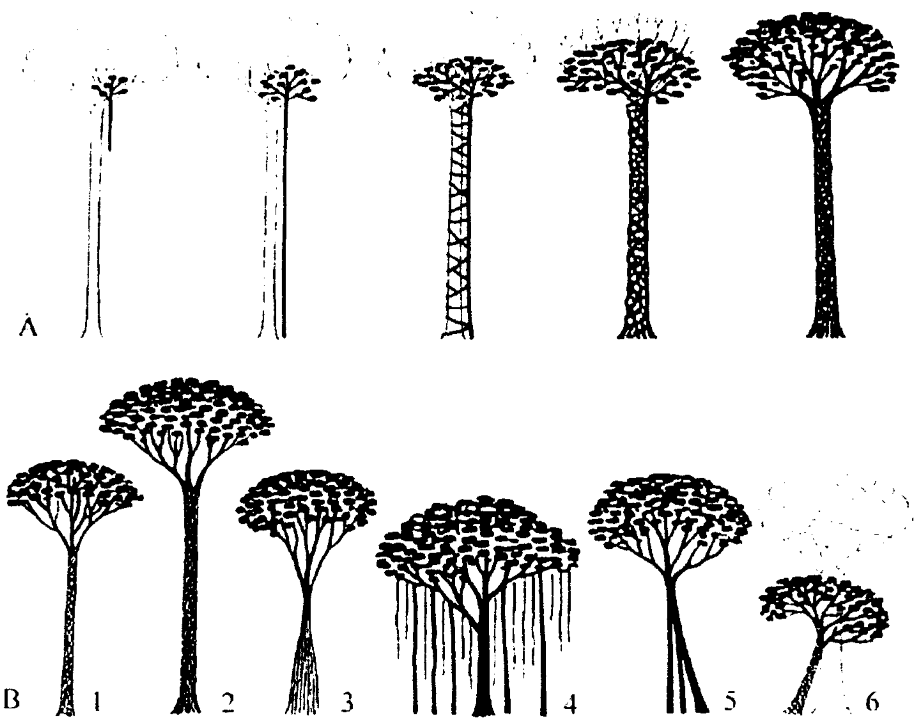


Figure 2.12 The pattern of hemi-epiphytic in subgenus *Urostigma*. A. Development from epiphyte and make the root basket around the host trunk, B. Form of root trunk; 1. meshy basket form 2. solid-wall basket form 3. longitudinally ribbed sheath 4. banyan-type 5. tripod type 6. ladder type (after Berg and Corner, 2005)

Hemi-epiphytic species are often found on the rock surfaces or on wall of building. Some species are only found on rocks called hemi-epilithic that may split the rocks. Some African species, *F. abutilifolia* (Miq.) Miq. and *F. tettensis* Hutch., are as 'rock-spitters'. Nearly 100 species of *Ficus* are climbers and the majority is species of subgenus *Synoecia* such as *F. pumila, F. pubigera, F. anserina,* etc. Not many fig trees are small shrubs, it usually represent in section *Sycidium* such as *F. heterophylla, F. montana* and *F. repens*. Some of them present 'lithophytes' growing on cracked rock. They are either grow in the arid or wet habitats, such as *F. montana, F. anserina* and *F. anastomosans*. The first species is a small shrub and the second species is a woody climber in moist forests, while the last species is a small shrub occurring on dry limestone mountain (Berg and Corner, 2005).

'Rheophytic shrubs' is a kind of habit that usually found in the riparian area with low bushy shrubs creeping stem in rocky beds of quickly running stream such as *F. squamosa* and *F. ischnopoda*. They form some adapted morphology to growing in running stream and also produced special fruit morphology for dispersal (Berg and Corner, 2005).

2.5.3 The leaves

The leaves vary in size, texture and margin. The smallest size is just a few centimeters whereas the largest is can be half a meter long (Figure 2.13). In *Urostigma*, the evident character of the leaves is coriaceous and entire margin, but the other groups are not. Some of them are chartaceous or subcoriaceous with a dentate to crenate margin. Those characters are related to their habit such as hairy surface, a chartaceous texture and a dentate margin, are usually represent in open and dry habitat.

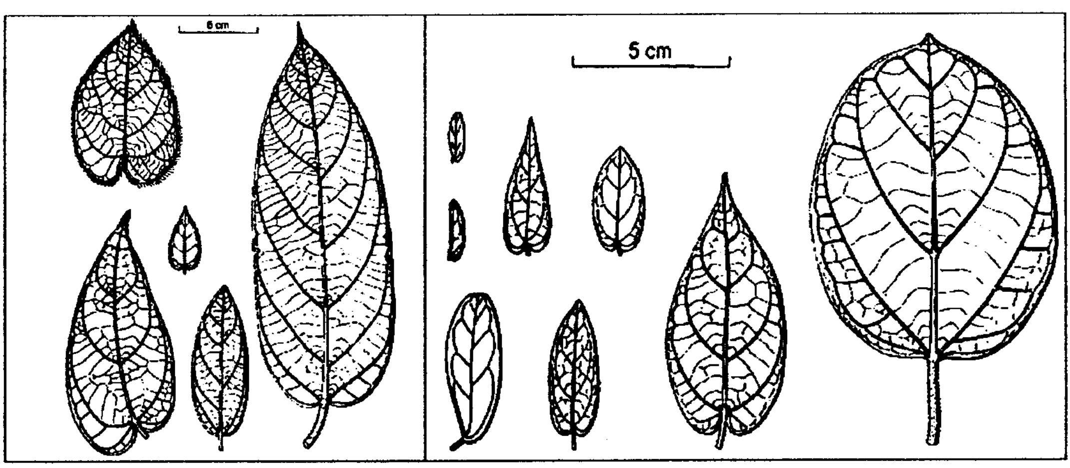


Figure 2.13 Variation on size, texture and shape of fig leaves (after Berg and Corner, 2005).

Normally, leaves are not the good character to use for classifying, but in *Ficus* there is one important thing on leaves. "Waxy or glandular spot" are commonly occurred on the lower surface of lamina, which is usually considered for separating the fig group. For example, in subgenus Urostigma, there is one waxy gland at the middle of the base of midrib, but in other groups this occurs in the axils of the basal lateral veins (Berg and Wiebes, 1992).

The characteristic of deciduousness of leaves evidently occur in subgenus *Urostigma* and seem to be absent in subgenus *Sycidium* and *Sycomorus* (Berg and Corner, 2005). Except in *F. racemosa* L., there are about 2 times per annum for this appearance (Wang *et al.*, 2005). The stipules are often fully amplexicual, and then leave annular scars.

2.5.4. The position and size of the figs

The position of inflorescence varies in this genus. The inflorescence or figs often born in leaf-axils but some born on the older wood, base of trunk, on leaf-less branches and some the branchlet become stolon-like for bearing syconium (geocarpic figs). "Fig size" is also diverse from a few millimeters (e.g. *F. lingua*) to more than 5 cm (up to 10 cm) in diameter. Commonly, there is a positive correlation between fig size and number of the flowers. The large size may contain thousands of florets inside. Fig size is not only related to the number of flowers, but also important to the pollination system such as the number of breeding sites for wasps, the number of fig wasps needs to occupy these sites (Berg and Wiebes, 1992).

2.5.5. The structure of the fig

The fig or inflorescence is believed to evolve from blending of the receptacle. They are usually fresh and have fruit like shape. Normally, the receptacle is subtended by a whorl of three or two basal bracts. In *Sycidium*, this basal is usually lacking. The margin of receptacle is not truly enclosed. It is a small hole between its receptacles, ostiole, of which the diameter varies. The bracts occur on the peduncle called 'peduncle bract'. Sometimes bracts occur on the outer surface of the receptacle ('lateral bracts'). Other technical terms of bract are "ostiolar" bract, in the entrance of the fig cavity; 'interfloral bracts'. The diameter of the ostiole varies, as well as the number of (visible) uppermost ostiolar bracts: two, three, or more in most groups all, or at least the upper ostiolar bracts are interlocking, from more or less tightly to more or less loosely. In several figs, the lower ostiolar bracts are descending, in the subgenus *Sycomorus* eventually forming a plug pressing on the developing (pistillate) flowers (Verkerke, 1989; Berg and Corner, 2005).

In the section *Galoglychia*, all ostiolar bracts are descending. The two outer most are large and the others are densely arrangement that leave a very narrow ostiole. In most cases, the bracts are so tight that pollinators can only enter with difficultly, and that escape is not possible. In the section *Sycidium*, however, the ostiolar bracts are more loosely interlocking, at least in the female and male phases, and fig wasps may escape without tunneling: this appears to represent a comparatively primitive state. The variation of ostiolar bracts are described by Verkerke (1989) (Figure 2.14).

The figs are pedunculate or sessile. In some species (e.g., *F. cyathistipuloides* and *F. densistipulata*) the receptacle is narrowed above the basal bracts into a 'stipe'. The receptacle is the wall of the syconium that varies in thickness, from less than one to more one cm, often relate to its size. The texture varies from solid and firm, to sometime spongy (*F. cyathistipula*). At full maturity the wall can become soft and free of latex, and the inner layers may become mucilaginous, and the wall is often colored: yellow, orange, pink, red or purplish. In many species the wall is spotted. In gynodioecious species 'gall figs' do not show the features of the mature 'seed figs', in which the wall become fleshy and colored. Ripe figs do not usually have pronounced smell, but those of *F. carica* L. do and also those of the subgenus *Sycomorus*. Ripe figs of *F. calyptrate* smell like rotten fish. (Berg and Wiebes, 1992)

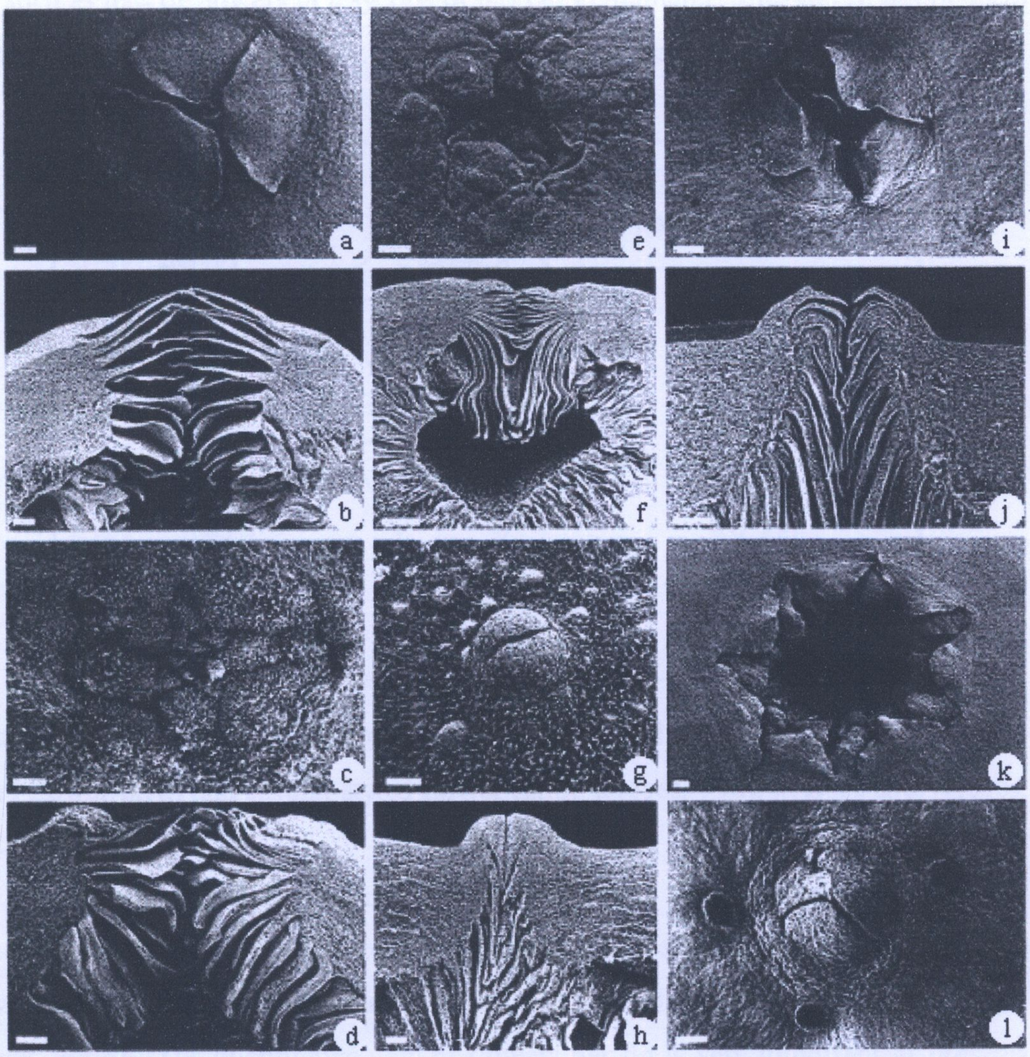


Figure 2.14 Top view and longitudinal section of various types of ostiole and ostiolar bracts; *a,b* subgenus *Ficus*; *c,d* *Sycidium*; *e,f Sycomorus*; *g,h Urostigma* section *Galoglychia*; *i,j,k* section *Pharmacosycea*; *l Urostigma* section *Americana*; bar indicates 500 µm. (after Verkerke, 1989)

2.5.6. The flowers/ inflorescences

Fig flowers are unisexual, except in some species of subgroup of *Sycidium*, in which the flowers are morphologically bisexual. Their flowers are presented both long and short-styled pistil (Figure 2.15) that the latter can support pollinator larva. The small flowers are packed in syconium. There are 2-5(7) free or connate tepals forming the tubular with glabrous. The number of the flowers per syconium increases with its size such as tens of flowers in a sycone of 0.5 cm in diameter, 300-400 of about 1 cm diameter, about 2,500 of about 2.5-3 cm, to several thousands in larger sycones.

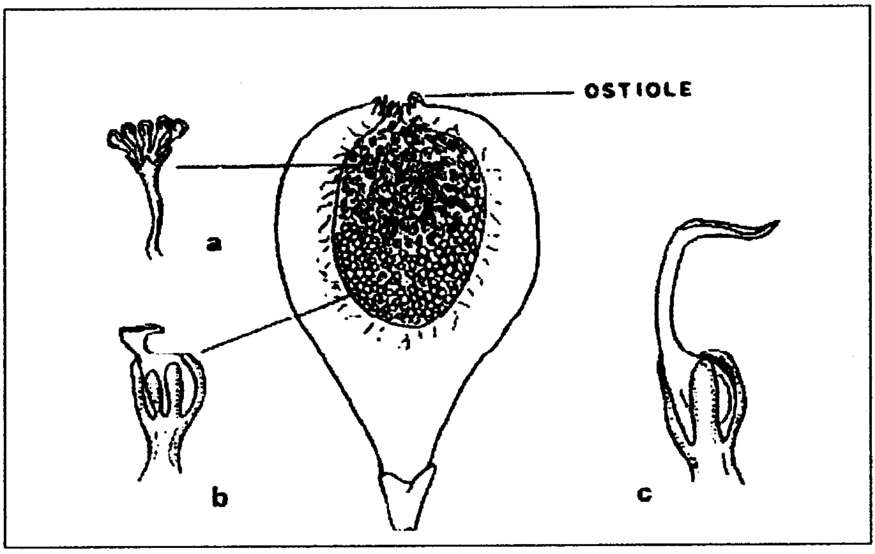


Figure 2.15 Longitudinal fig sycone. *a.* staminate and pistillate flowers: *b.* short-styled flower (gall) and *c.* long-styled flower (after Wiebes, 1982 in Berg and Wiebes, 1992).

In gynodioecious figs, sometimes can find neuter flowers represent in gall figs that often found in subgenus *Synoecia*. The 'neuter flower' is the long-styled pistillate flowers as substitutes for staminate flowers and consist of reduce tepals (Berg and Corner, 2005). The quantitative data of flowers per fig is very important. It presents the number of seeds, bladders, gall and also pollen grains (Compton and Nefdt, 1990; Berg and Wiebes, 1992). However, the composition varies in different sections.

A. The staminate flowers

The staminate flowers are found in two pattern of arrangement, one is dispersed among the pistillate flowers (usually in monoecious group) and the other is arranged in one or several rows near the ostiole, which usually occurred in gynodioecious species (Verkerke, 1989; Berg and Wiebes, 1992). The number of stamen is one, two or sometimes three in each flower and usually surrounded by some simple and free perianth segments. The pattern of unistaminate and bistaminate condition is an important taxonomic feature. The anthers mostly have four loculi arranged to a pair thecae and is dorsally attached. It is about 0.5-1 mm long, but in species of genus *Sycomorus* mostly 1-1.5 mm long. Dehiscence is usually through the longitudinal slit. Within the genus, the pollen is rather uniform; is ellipsoidal, measuring 11x6 µm, with a smooth exine and two apical germ pores, when shed it is two-celled and contains starch grains (Verkerke, 1989; Figure 2.16).

The staminate flowers of subgenus *Sycomorus* are distinct from those of the other subdivisions. The stamens become exposed by elongation of the filaments, by which the upper part of the perianth is torn open or off. The flowers are initially entirely or partly enveloped by two bracteoles. In subgenus *Urostigma*, staminate flowers are dispersed among the pistillate flowers. They are more or less hidden by these flowers and underneath the synstigma.

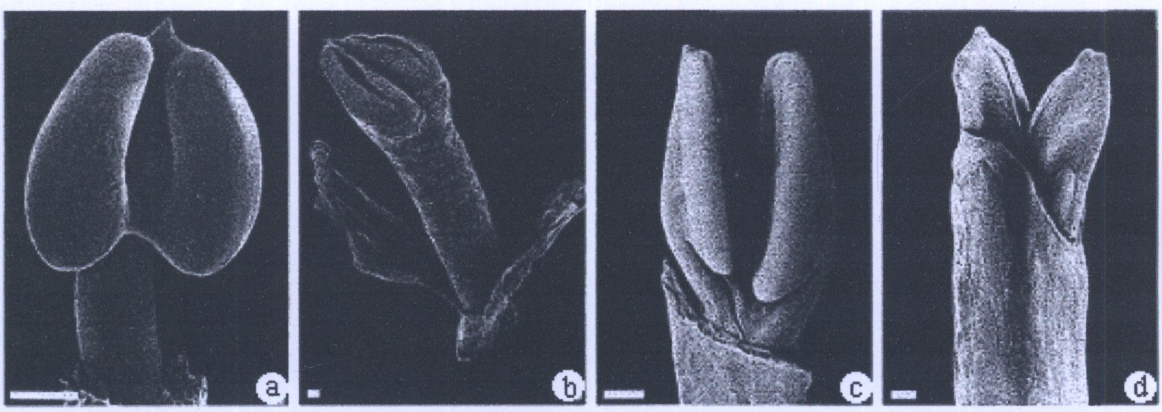


Figure 2.16 Staminate flower (perianth removed); *a, b Urostigma* section *Galoglychia* (perianth removed), *c* section *Pharmacosycea*, *d* section *Sycomorus*; bar indicates 200 µm (after Verkerke, 1989).

B. The pistillate flowers

There are diverse styles both length and shape and even ovaries of pistillate flowers (Bronstein, 1988; Compton and Nefdt, 1990; Berg and Wiebes, 1992). The shapes of stigma are various such as two filiform (subgenus *Urostigma*), subulate, infundibuliform (section *Sycidium*), subclavate to tongue-shaped (subgenus *Sycomorus*). The stigma are mainly line up on the inner wall as one plane which stigmas touching each other, adnate or cohering called 'synstigma', the pattern is unlikely in different subgenus or section (Figure 2.17). As well as the ovaries are often different in shape and length such as ovoid, oblongoid or obovoid with or without a stipitate base (Verkerke, 1989; Berg and Wiebes, 1992)

In monoecious, style length is several layers. Wasps prefer to oviposit in shorter style flowers that located close to the cavity, whereas longer styled flowers, located closed to the fig wall, mainly produce seeds (Jousellin *et al.* 2001, 2003). All pistillate flowers can produce seeds (if oviposition). On the other hand, not all ovaries can be occupied by larva that may be caused by the styled length or the number of foundress and number of eggs carried (Bronstein, 1988; Compton & Nefdt, 1990; Michalound 1988b; Berg and Wiebes, 1992). The variation of pistillate was described in Verkerke (1989) (Figure 2.18).

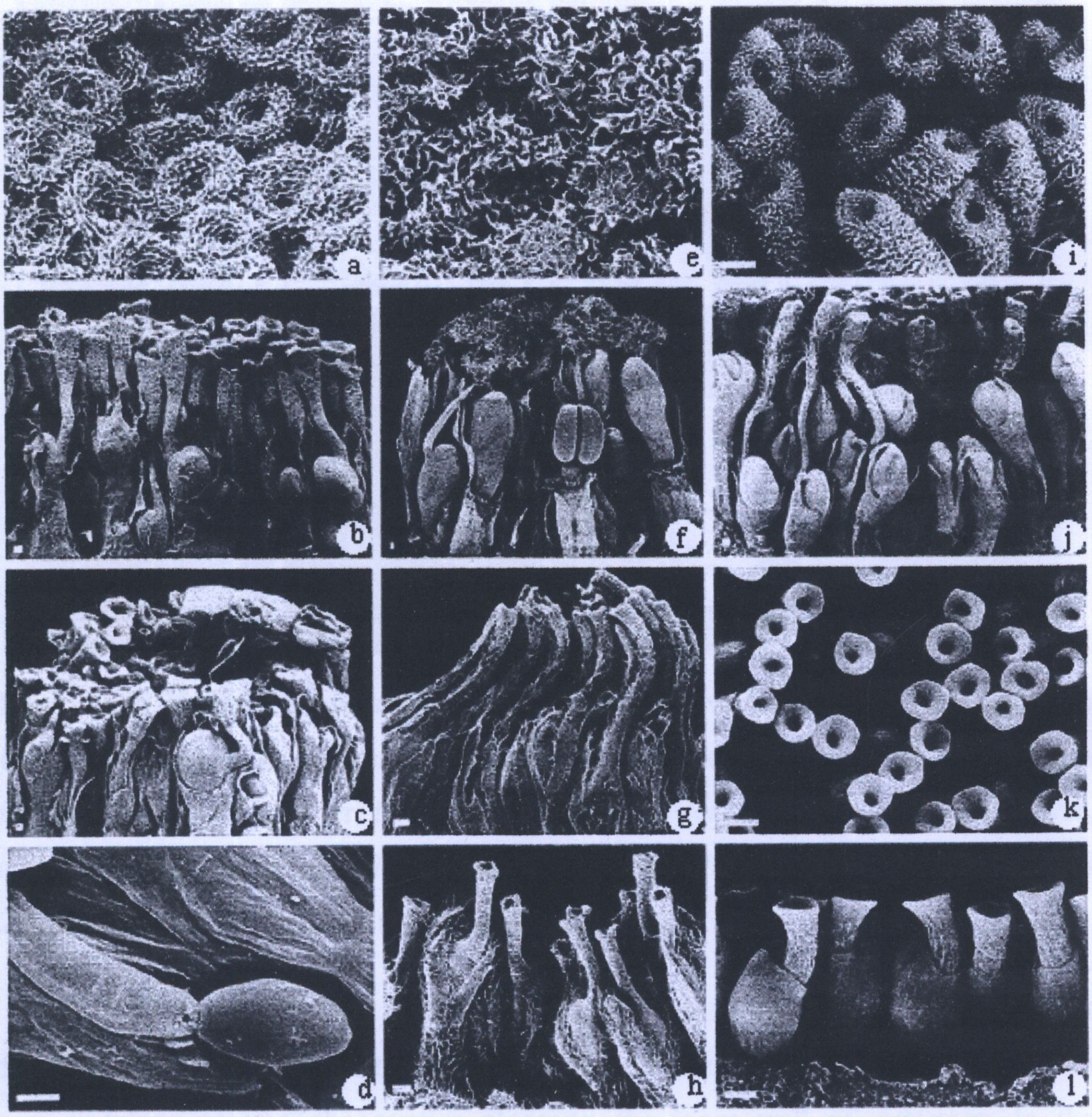


Figure 2.17 Female flower; surface and lateral view; *a-f* monoecious figs; *g-l* gynodioecious figs; *a-d* section *Sycomorus*, *c* ovipositing *Ceratosolen* spp.; *d* germinating pollen grain; *e-f Urostigma* section *Galoglychia*; *g,h Sycidium*, seed flower and gall flower; *I,j Neomorphe*, seed flower; *k,l Sycocarpus*, gall flowers; bar indicates 100 µm (a-c, j-l), 5 µm (d), and 200 µm (e-h) (after Verkerke, 1989).

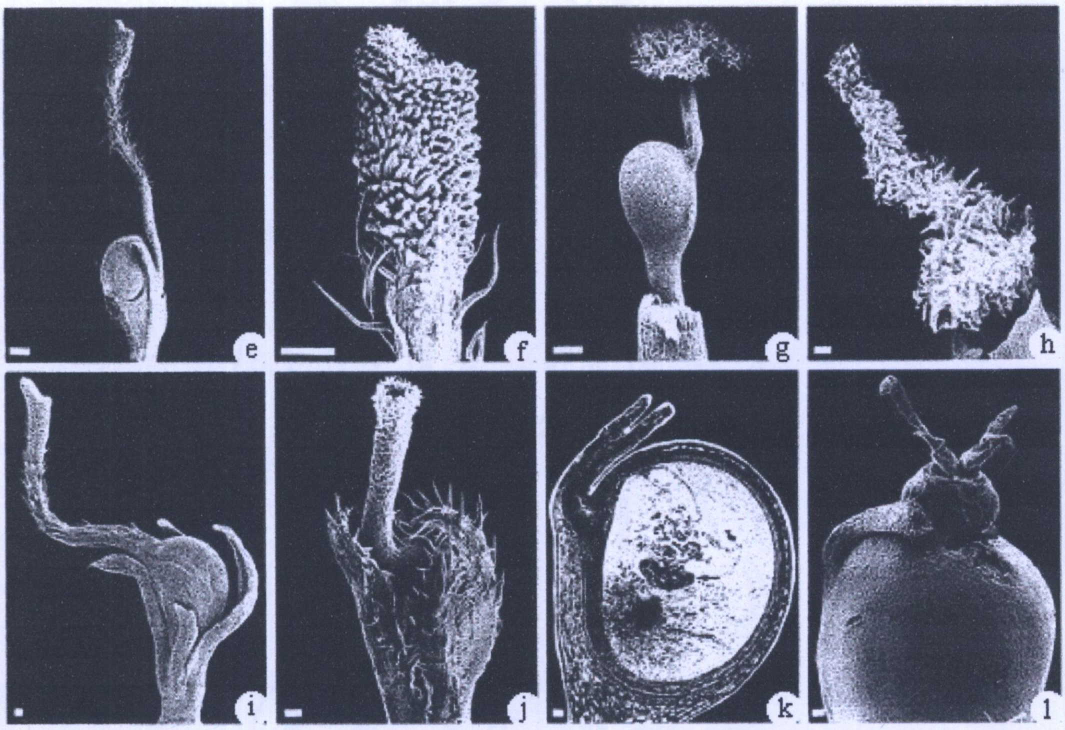


Figure 2.18 Pistillate flowers; *e,f Neomorphe* seed flower, and detail of stigma, *g,h Urostigma* section *Galoglychia*, short-styled flower (perianth removed); and stigma from the long-styled flower, *i-l Sycidium*; *i* seed flower, *j* gall flower; *k* gall flower, arrow indicating wasp larva, *l Kradibia* sp. Emerging from gall flower; bar indicates 200 µm. (*e*) and 100 µm. (*f-l*) (after Verkerke, 1989).

Normally, up to 10% of the female flowers fail to develop fruits, and about 50% of the developing fruits contain seeds and the remaining insect larvae. In gynodioecious species, the ovaries place on the inner wall of syconium in the distance. The stigmas form continuous layer, but not always clearly synstigmatic pattern. After anthesis, the developing fruits become arranged in some layers. All long-styled flowers can produce seed (Berg and Wiebes, 1992). The variation of fruits and seeds were described by Berg and Corner (2005) (Figure 2.19)

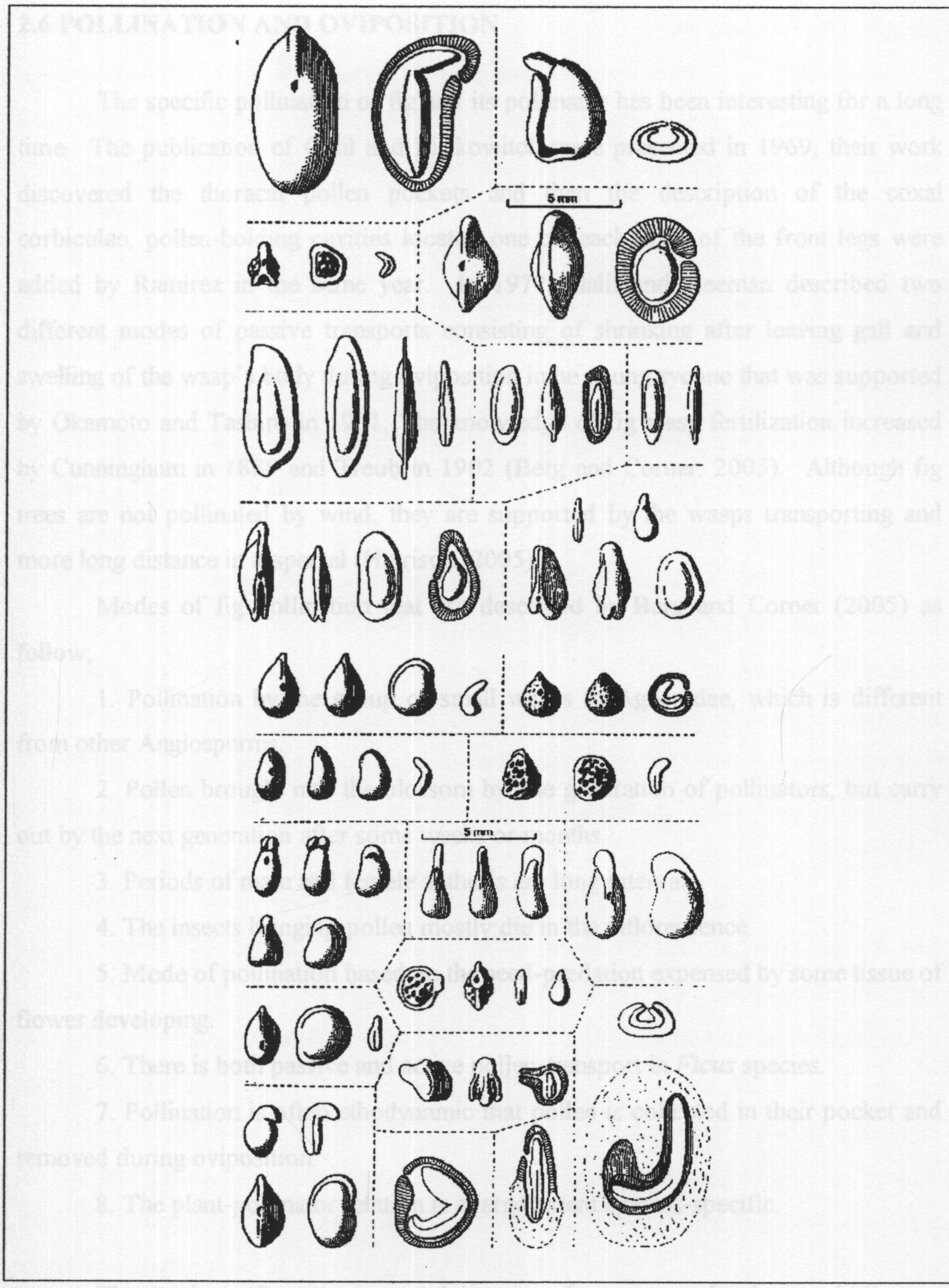


Figure 2.19 Variation of fruits (achenes) and seeds in *Ficus* spp. (after Berg and Corner, 2005).

2.6 POLLINATION AND OVIPOSITION

The specific pollination of fig and its pollinator has been interesting for a long time. The publication of Galil and Eisikowitch were presented in 1969, their work discovered the thoracal pollen pockets and then the description of the coxal corbiculae, pollen-holding cavities located one on each coax of the front legs were added by Ramirez in the same year. In 1977, Galil and Neeman described two different modes of passive transports consisting of shrinking after leaving gall and swelling of the wasp's body during oviposition in he young sycone that was supported by Okamoto and Tashiro in 1981. The knowledge of fig wasp fertilization increased by Cunningham in 1889 and Treub in 1902 (Berg and Corner, 2005). Although fig trees are not pollinated by wind, they are supported by the wasps transporting and more long distance in dispersal (Harrison, 2005).

Modes of fig pollination that are described by Berg and Corner (2005) as follow;

1. Pollination by the group of small wasps in Agaonidae, which is different from other Angiosperms.
2. Pollen brought into the blossom by one generation of pollinators, but carry out by the next generation after some weeks or months.
3. Periods of male and female anthesis are long interval.
4. The insects bringing pollen mostly die in the inflorescence.
5. Mode of pollination based on the seed-predation expensed by some tissue of flower developing.
6. There is both passive and active pollen-transport in *Ficus* species.
7. Pollination is often ethodynamic that pollen is collected in their pocket and removed during oviposition.
8. The plant-pollinator relation is a large extent species-specific.

The numbers of monoecious and dioecious figs are regard to be equal in nature (Berg, 1989). Monoecious fig produces both seeds and wasps in the same syconium. Unlikely in dioecious fig, male tree produce wasps offspring and female trees produce seeds (Berg, 1989; Kjellberg *et al.* 2005). Inside the syconium, monoecious species contains male and female flowers with different style-lengths that distinguish occurrence: short-style and long-style or sometimes intermediates called 'imperfect heterostyly' and all female flowers can produce seeds in this case. In dioecious species, female flowers in male trees have short style, on the other hand in female tree only long style represent, it is 'perfect heterostyly' (Berg, 2003a). The sex ratio of flowers tends to promote to strong more female number, often about ten times that female more than male flowers. Some male floret scattered in syconium, but some species, it is located near the ostiole. (Verkerke, 1989).

The main reason of difference between female flowers in functional monoecious and dioecious figs is likely caused by the style length. Female pollinators can probe in both groups but in short-styled flower (gall) they can success of laying eggs, contrastingly in the long-styled flowers they can only probe but the ovipositor cannot reach fig ovule (Nefdt and Compton, 1996; Kjellberg *et al.*, 2005).

The typical pollination and oviposition that Galil and Eisikowitch (1968) described is between *Ceratosolen arabicus* and its host, *Ficus sycomorus*. When the foundress enters the receptive fig, she stands on the synstigma and probes with her ovipositor. The ovipositor moves downwards along the style and the fore legs take some pollen to touch the stigmatic surface and the pollination begins (Figure 2.20).

Kjellberg *et al.* (2005) described that when the fig is receptive, a specific odor is produced to attract female pollinator. She comes with pollen and enters the fig via ostiole. Inside the syconium, the female wasp walks on the stigmatic surface and pollinate them; together with oviposit its eggs through the style. Therefore, if the style is too long, no egg is deposited. Then the female dies and each wasp larva develops in each female floret.

After pollination, the pollen tube grows through the stylae canal and through the micropyle into the embryo-sac. The embryo develops and endosperm is formed. The egg is deposited in the fig-ovule, outside the nucellus and beneath the insert point of the inner integument at the raphal side (Verkerke, 1988).

In this plant group, there are two modes of pollination; active and passive represent. 'Active pollination' is the mode that pollinators collect pollen from their natal fig into pollen pocket. The wasps leave their natal fig to search of a new receptive fig for oviposition. They will lay an egg in ovule as well as deposits pollen grains on the stigma (Galil and Eisikowitch, 1969 in Jousselin and Kjellberg, 2001). 'Passive pollination' is the mode of collecting pollen, but deposition is not present.

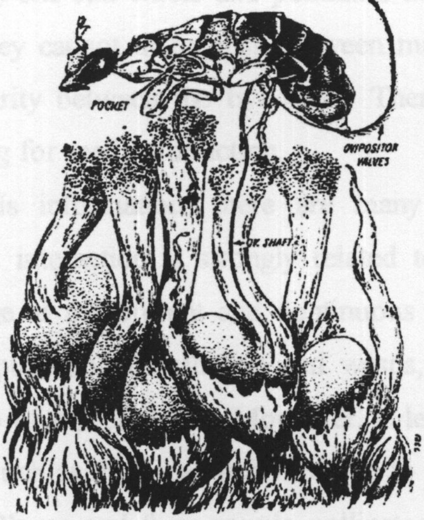


Figure 2.20 *Ceratosolen arabicus* Mayr and its host, *Ficus sycomorus* during oviposition and pollination. (after Galil and Eisikowitch, 1968)

The actively pollinated figs usually produce lesser in the number of pollen grains while passive pollination fig produce a large number of pollen grains that released by anther dehiscence (Galil and Neeman, 1977; Galil and Meiri, 1981; Kjellberg *et al*., 2001 in Kjellberg *et al*., 2005). In female figs, wasps don't lay eggs but they still probe some pollen in each time of laying (Galil, 1973; Balakrishnan and Abdurahiman, 1987 in Kjellberg *et al*., 2005). One-third of *Ficus* has passive pollination syndrome (Kjellberg *et al*., 2005).

The numbers of pollen grains that can be carried in pollen pocket depend on species, for example, 1000 in *F. religiosa* and 2,000-3,000 in *F. sycomorus* (Galil and Snitzer-Pasternak, 1970; Galil and Eisikowitch, 1968 in Kjellberg *et al*., 2005).

It is believed that active pollination has evolved from monoecious to dioecious. The benefit of fertilization of female flowers can serve the pollinator larvae. Therefore, each female flower is oviposited by foundress, pollination and found. In case of studies on other actively pollinating insect implied that it has evolved from seed eating. But in fig and fig wasp, it seems to have evolved from ovule parasitism (Jousselin and Kjellberg, 2001).

In female dioecious plant, it seems to be non beneficial for pollinators to enter to pollinate fig, then why she still enters and pollinates them? Moore *et al.* (2003) reported that because they cannot distinguish between male and female figs, which resulted from the similarity between the two figs. Therefore, they may attend to evolve this trait benefiting for seeds production.

According to this information, there are many factors to affecting this interaction and also this interaction is strongly related to other biotics in tropical ecology. Climate change at the present and continuous forest destruction that are critical to change in population of both figs and wasps, periods of flowering and fruiting and also balance of reproduction. Moreover, it leads to change in the long-term evolution of them such as the break down of one to one specific relationship in *F. fistulosa* Reinw ex. Blume and their couple pollinators represented *Ceratosolen constritus* (Mayr) in Java and Sumatra and *C. hewitti* Waterston in Borneo and Java (Wiebes, 1979) that caused by changing of geographical landscape.

Many researches suggested to the ancestry way of fig-wasp mutualism. Wiebes (1979) proposed those ideas of evolving in his work, he suggested in 1963 that the agaonid wasps could have reduced size from other gall-forming or parasite Chalcidoidea living together with flowers or seeds of pre-*Ficus*. Whereas Ramirez (1976) suggested that the agaonids evolved from pollen-feeding gall-makers and described the way to produce pollen pocket. The extra organ may evolve from digestive tract, which was found carrying pollen.

Chemical release is the one of the important factors that figs use for attracting their pollinators. It was found that they have a specific chemical in each plant species. In figs and wasps, they are some reports on volatile emission. In dioecious species, male and female figs need the same pollinator to probe, so they should release the same volatile as well. Grison-Pige' *et al.* (2001) studied the chemical release from *F. carica* in both male and female figs, it is shown that the male and female figs emitted the same compound, but differs between quantities and proportions.

There is no difference in style length between tree within a species (*F. microcarpa and F. citrifolia*) and the style length does not determine if a pollinated flower will be a seed or wasp producer but it may be reduce the probability of pollination (Otero, 2002).

The ovipositor may be too short for the long-styled flowers and/or the long styles maybe too slender, too flexible or too much curved. There may be also other reasons, such as the number of eggs carried by the pollinator, the number of species of pollinator, etc. (Bronstein, 1988; Compton & Nefdt, 1990; Michalound 1988).

2.7 EVOLUTION OF POLLINATION AND OVIPOSITION

2.7.1 Mutualism and co-evolution

2.7.1.1 Species-specific relations of Fig and wasp

The specific interaction of figs and their pollinators has been classified at least in the level of subgenera even at the levels of sections and/or subsections (Table 2.4). However, they are few cases that the wasp genus does not match the subgenera or section of *Ficus*. For example *F. asperiuscula* Kunth& C.D. Bouche' and *F. complexa* Corner (subgenus *Sycidium* sect. *Sycidium*) *Ceratosolen* instead of *Kradibia* or *F. montana* Burm.f. (subgenus *Sycidium* sect. *Sycidium*) *Liporrhopalum* instead of *Kradibia* (Berg, 2003a).

2.7.1.2 Some theories and hypotheses of fig and fig wasp interaction

One to one species theory

It is generally known that the relationship between fig and fig wasp is a specific association. One to one species relationship is the important reason that places it to be the most type of co-evolution studied. Most of fig trees are believed to have their own specific pollinator and many publications supported this. Berg and Wiebes (1992) reported that figs in Africa have their own wasp pollinators. Some hypotheses supported one-to-one species such as the length of style, hole size and ostiolar bracts pattern, specific chemical release, etc.

Attracting chemical released from each fig species is claimed to be specific. Each fig tree releases a particular volatile to attract its pollinator and also have unique volatile profile (Ware *et al.*, 1993; Weiblen, 2002).

TABLE 2.4 Hymenoptera reared from fig inflorescences, in alphabetical order (Weiblen, 2002)

Family	Subfamily	Genera (number of described species)
Agaonidae	Agaoninae	*Agaon* (11), *Alfonsiella* (7), *Allotriozoon* (3), *Blastophaga* (24), *Ceratosolen* (61), *Courtiella* (13), *Deliagaon* (4), *Dolichoris* (10), *Elisabethiella* (14), *Eupristina* (13), *Liporrhopalum* (18), *Kradibia* (23), *Nigeriella* (4), *Paragaon* (2), *Pegoscapus* (45), *Platsyscapa* (19), *Pleistodontes* (18), *Tetrapus* (6), *Waterstoniella* (20), *Wiebesia* (18)
	Epichrysomallinae	*Acophila* (2), *Asycobia* (1), *Camarothorax* (6), *Eufroggattisca* (1), *Epichrysomalla* (1), *Herodotia* (2), *Meselatus* (4), *Neosycophila* (2), *Odontofroggatia* (4)
	Otitesellinae	*Aepocerus* (19), *Eujacobsonia* (2), *Grandiana* (3), *Grasseiana* (2), *Guadalia* (1), *Heterandrium* (9), *Lipothymus* (4), *Marginalia* (1), *Micranisa* (5), *Micrognathophora* (1), *Otitsella* (18), *Philosycella* (1), *Walkerella* (»5)
	Sycoecinae	*Crossogaster* (16), *Diaziella* (12), *Philocaenus* (22), *Robertsia* (2), *Seres* (5), *Sycoecus* (10)
	Sycophaginae	*Anidarnes* (3), *Apocryptophagus* (»30), *Eukobelea* (4), *Idarnes* (15), *Pseudidarnes* (5)
	Sycoryctinae	*Adiyodiella* (1), *Apocrypta* (24), *Arachonia* (1), *Dobunabaa* (1), *Philotrypesis* (»50), *Philoverdance* (1), *Sycoryctes* (4), *Sycoscapter* (46), *Sycoscapteridea* (4), *Tenka* (1), *Watshamiella* (»10)
Braconidae		*Ficobracon* (1), *Psenobolus* (3)
Eurytomidae		*Bruchophagus* (1), *Eurytoma* (1), *Sycophila* (3)
Orymidae		*Orymus* (2)
Pteromalidae		*Hansonia* (1), *Podivna* (1)
Torymidae		*Physothorax* (7), *Torymus* (1)

Song *et al.* (2001) reported that volatiles from *Ficus hispida* L., the major distilled oil of either male or female receptive figs, was linalool while dibutyl phthalate was the major compound of the oils of post parasitized and post pollinated figs. However, some situations of fig tree show that cospeciation is not always the rule.

2.7.1.3 Non-species specific

Although some studies found that more than one pollinators co-occurrence in the same figs, it is a few out of a hundred of fig trees around the world.

A. One species of fig and more than one wasp

Ficus sycomorus, the widely distributed tree in Africa, presents two species of wasps- *Ceratosolen arabicus* and *C. galili* Wiebes. The former wasp proved to be its pollinator, while the latter acted as a cuckoo, ovipositing in the flowers without pollination (Wiebes, 1979). Another case also in Africa which is represented by two sympatric species, *Ceratosolen silvestrianus* and *C. arabicus,* and *Ficus sur*. They are both active pollinators and may be found together in the same syconium without oviposit competition (Kerdelhue' and Rasplus, 1997). However, not many cases occurr.

B. One species of wasp and more than one fig

The association of one wasp and two or three figs were published such as *Ficus soroceoides* Baker from Madagascar and *F. laterfolia* Vahl from R'eunion both associated with *Kradibia cowani* Saunders

The interesting contrast between Herre (1989) and Bronstein and McKey (1989) who studied among-species and within-species of *Ficus* is the studies among species shows that smaller fig has fewer number of flowers and foundresses, whereas within species found that both small and large fig size has similar numbers of flowers but different in foundresses number (Frank, 1989).

In the theory of co-evolution between figs and fig wasps, "one-to-one" is considered. Many scientists have been studying their interaction. Yang *et al.* (2002) addressed pollination biology of *Ficus hispida* L. in tropical rainforest of Xishuangbanna, China. The result showed that only one or two fig wasps (not over 4) entering one female syconium. The ratios of seeds to total female florets were 51.3 % (at one pollinator) and 86.5 % (at two pollinators). On the other hand, when the number of the fig wasps entering the syconium was up to 4 or more, the amount of seeds developed decreased.

The crop size of pollinator depends on its number of eggs laid, usually 100-400 depending on size of insect. The ratio of male and female insects varies from 0.1 to 0.4 (Berg and Corner, 2005). The percentage of florets developing into seeds and wasps varied considerably between crops, even on the same plants, so comparisons between species and between breeding systems are difficult (Corlett *et al.*, 1990).

Not only pollinators associated with figs, but also other wasps that function as non-pollinators. There are a great number of species represented, sometimes up to thirty, in only one fig species (Compton and Hawkins, 1992). They almost breed in fig flowers; some are gall-maker, which oviposit in vacant ovaries by the fig cavity or by using long ovipositor from outside a syconium after pollination occurred. 'The parasite wasps' means their lava directly feed on another developing larva, while 'the inquilines' is the insect which their larva feed on the gall plant tissue. (Kerdelhue' and Rasplus, 1996) Most dioecy clearly present a seed and offspring syconium on male and female plants. On the other hand, for monoecy, both seeds and offspring are produced in the same syconium.

The pattern of progeny product was illustrated in *Ficus sur*, a monoecious species (Kerdelhue' and Rasplus, 1996). The inner short-styled flower ovaries are mostly occupied by larvae of pollinators, *Ceratosolen*. *Sycophaga* (gall-maker) and by their parasites mainly develop in the second layer, but some of gall-maker also found (*Apocryptophagus*). The third layer produce a few seeds and mainly of *Apocryptophagus* which lay eggs from outside. The outer layer is the seed layer, but some of *Sycophaga* and *Apocryptophagus* can be found (Figure 2.21).

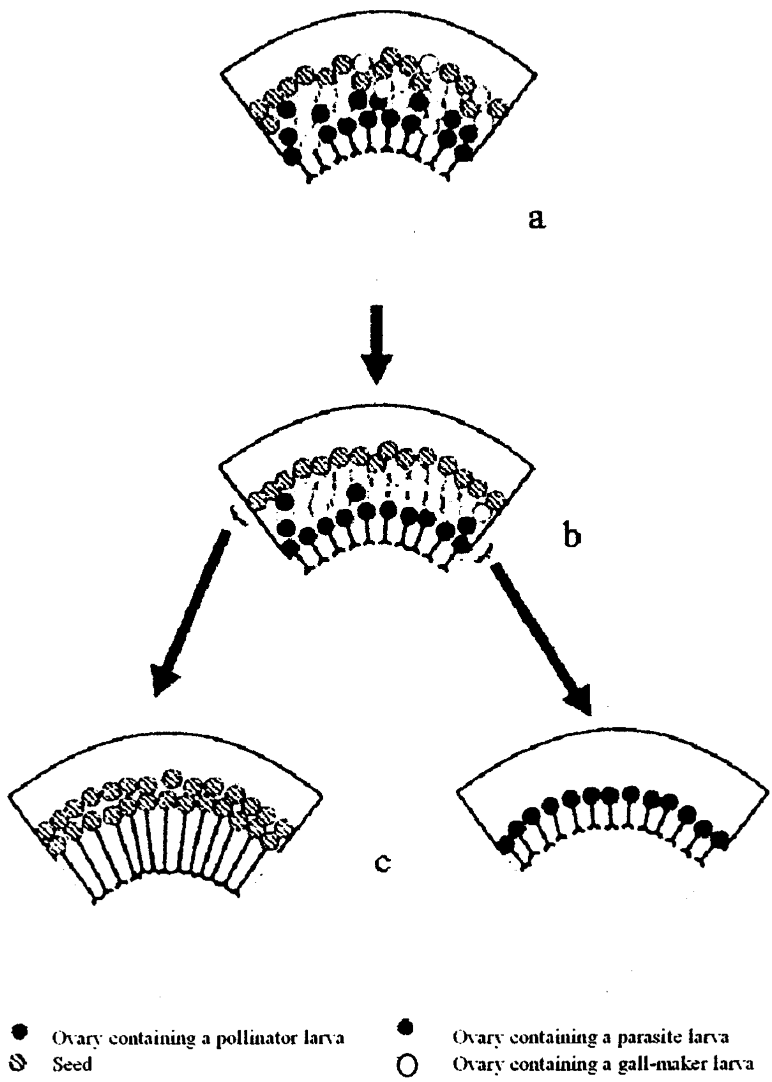


Figure 2.21 The evolution pattern of oviposition in dioecy and monoecy fig tree. *a.* pattern in monoecy figs, b. representation of non pollinating wasp in medium layer and c. evolution towards dioecy figs which separate to male and female trees (after Kerdelhue' and Rasplus, 1996)

2.7.2 Fig and wasp – Adaptations

Such a long time for the evolution, at least 90 million years ago, of figs and wasps, they both have adaptation together. Fig trees show diverse phenology and distribution as well as their pollinators represent. Many characters were evolved for this mutualism such as their chemical release, morphology and physiology. Several publications found that figs particularly discharge the unique volatile oil to attract their specific pollinators. Also, several morphological characters present to evolve adaptation such as the varieties of ostiole and ostiolar bracts arrangement that believed to protect flowers from non benefit insects and extra wasps entering (Verkerke, 1989).

The shape (more slender) and length of style (long style flowers) in pistillate flowers may be in order to maintain the stable of seeds and wasps production (Corlett *et al.*, 1990). Another stage seems to maintain fig and wasp population is asynchrony of flowering and fruiting fig trees (Winsor *et al.*, 1989). Normally, phenology is described as synchronous within each crown of an individual and asynchronous among individuals (Frank, 1989). Therefore, the representation of asynchrony of each individual is referred to supply wasps' oviposition in case of few fig tree populations in the area (Kjellberg and Maurice, 1989).

Some figs have adaptive pollination system. It may protect insect larva and pollinative function such as watering in subgenus *Sycomorus* (Berg and Corner, 2005). Whereas an active pollination mode seems to benefit wasps because they support flowers to improve the nutrition for larva surviving and more increasing success of gall initiation (Jousselin and Kjellberg, 2001; Jousselin *et al.* 2003). The Females wasps have fore and hind legs strong and spiny to help pushing the head forward when enter the figs (Berg and Wiebes, 1992). Another special part is 'pollen pocket' evolved on thoracic structure (Kjellberg *et al.*, 2001)

2.8 PHYLOGENETIC STUDY

The relationship between fig trees and wasps is dominantly are aimed for studies in evolution. Not many reports in molecular phylogenies established. Comparisons of fig and pollinator phylogenies at taxonomic levels have supported cospeciation, for instance, several monophyletic genera of pollinations are uniquely associated with host sections including *Blastophaga* with *Ficus, Platyscapa*, with *Urostigma* and *Pleistodontes* with *Malvanthera* (Weiblen *et al.*, 2001).

Kjellberg *et al.* (2005) concluded some of preliminary studies; (1) monophyly of *Ficus* and of fig-pollinating wasps (2) monophyly of *Ficus* sections and agaonid genera (3) nonparallel branching order of agaonid genera and *Ficus* sections and (4) some support for fine scale cospeciation of wasps and *Ficus*. However, they suggested that the molecular evidence point (3) is weak. Its result shows that *Ficus* can be divided into two strongly supported lineages (Figure 2.22), a basal one containing section *Pharmacosycea* and two groups of equal rank; group1 (subsection *Urostigma* except section *Urostigma*) and group 2 (all other species, i.e. section *Oreosycea* (Subgenus *Pharmacosycea*), section *Urostigma* (subgenus *Urostigma*), subgenus *Sycomorus* and subgenus *Ficus*)

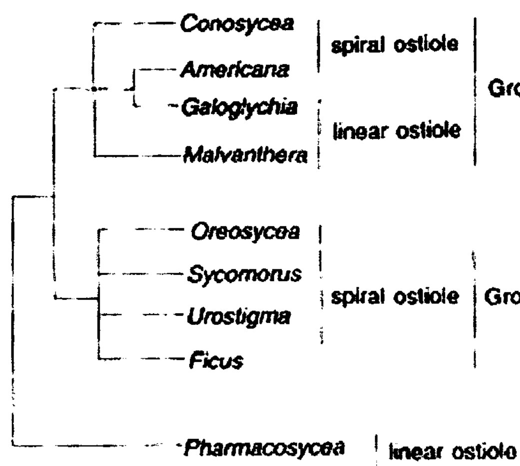


Figure 2.22 A molecular phylogeny of *Ficus*, two monophyletic groups are defined; group 1, group 2 and the outgroup, section *Pharmacosycea*. Spiral ostioles seem to have evolved three times independently (after Kjellberg *et al.*, 2005).

2.9 DISPERSAL

Many fig species are pioneers and play a significant role in forest succession in the tropics (Corner, 1967 in Harrison, 2005). The majority of fig dispersal is by animals. Many kinds of animals feed on these fruits such as monkeys, squirrels, fruit bats and also birds. Some eat and drop while some of them may carry figs to other places. The colours of ripe figs are varied from green to yellow, orange, red, purple or blackish. That may attract their feeders to help them for expanding the next generation (Berg and Corner, 2005). There are both biter and swallower consumers, which depend on size of figs (Peh and Chong, 2003).

Besides animals, some figs growing nearby the river are dispersed by water. For instance, an adaptation of fig floating is forming thick spongy wall of the syconium in *Ficus cyathistipula*. For some rheophytic species, *F. macrostyla and F. squamosa*, the very long style persistent with short and stiff retrose hairs will lead the fruitlets to attach the substrate (Berg and Corner, 2005).

An incredible number of vertebrates over 1,200 species feed on figs because of the year-round fruit product. Fig population may be critically worth to wildlife when without other fruits (Shanahan, 2001a). Not only vertebrate frugivores function as seed dispersers, but also invertebrates such as ants, dung beetles, snails and hermit crabs (Kaufmann *et al.*, 1991; Athreya, 1996; Laman, 1996; Davis and Sutton, 1997; Shanahan, 2000; Staddon, 2000 in Shanahan, 2001a)

Peh and Chong (2003) studied seed dispersal agents of *F. fistulosa* and *F. glossularoides* in Bukit Timah Nature Reserve, mainland of Singapore. It is found that the primary dispersal agents of *F. fistulosa* are mainly terrestrial mammals and bats (commonly biters) but some were relative to the large birds such as Great Hornbill and Pink-necked Pigeons. The high quality fig dispersers of it were the Black-naped Oriole, Asian Glossy Starling and long-tailed Macaque. Whereas *F. glossularoides,* that fig size is smaller than *F. fistulosa*, has a wide range of fig eating birds. Its high quality fig dispersers are the Red-Crowned Barbet, Coppersmith Barbet, Scarlet-backed Flower-pecker, Asian Fairy Bulbul, etc.

The fruit characters of fig trees and frugivores were compared in the colonization of island volcano, Long Island, Papua New Guinea, and an emergent island, Motmot. It was shown that the different fig phenologies affect different kinds of dispersers. Fig species reveal two broad dispersal types; the first group produces large and green figs in the lower level of the forest and attracts fruit bats. The second group includes species that produce smaller and red fruits to attract both birds and fruit bats (Shanahan *et al.*, 2001b). Normally, fruit bats eat mostly ripe figs and defecate the seeds in flight. Seeds that pass through their guts have enhanced germination (Handley *et al.*, 1991; Kalko *et al.* 1996; Fleming *et al.*, 1982 *in* Banack *et al.* 2002).

Marduka (2001) studied birds and mammals visiting a fruiting fig at Niah National Park of Malaysia. It was found that *Ficus benjamina* L. was used by a large number of small birds and other fruit-eating animals. There were more than 500 birds feeding on fig fruits in the early morning from 06.00 am to 10.45 am. Bird species such as barbet, black hornbills, glossy starling, green pigeon, Hill myna and a few insectivorous birds were encountered around the fig tree, possibly feeding on insects attracted by fig fruits such as white-rumped shama and spider hunter. However, there were a few of big birds and big animals feeding on fruits, perhaps because the fruits were too small (7 to 8 mm in diameter) for them.

Some riparian fig trees are not mainly dispersed by birds but by fruit eating fish such as *F. insipida* which establish along streams, its major dispersers are both bats (*Artibeus spp.*) and some fishes (*Brycon guatemalensis* Regan) (Banack *et al.*, 2002). In addition, the same fish species was reported to be a good disperser of *F. glabrata*, which can carry the large number of seeds and help maintain the upstream plant population (Horn, 1997).

Dispersers are the important factor to support fig trees to succeed in their distribution, especially the animal vectors that can lead their colony to establish long distance from their mother tree (Harrison, 2005). The diversity of figs arises at least caused by their dispersers and also fig-eater arises because of the widespread distribution, year round production and attractive fruit characters of figs (Shanahan, 2001a). These relations can be an invaluable tourism resource for wherever that visitors can do bird watching when fig trees are fruiting (Marduka, 2001). Hence, the relationship between figs and their dispersers is one of an evolved mutualism with an important issue to investigate.

2.10 GERMINATION

There are not many reports of fig germination. Like other plants, general things for growing and development are both environmental and genetic factors. Germination of most *Urositgma* requires light while other groups need less. The fig seeds usually have mucilage exocarp that may inhibit germination, so that a process of passing fruits through the bird digestive tract may be a positive effect in speeding germination (Ramirez, 1976; Berg and Corner, 2005).

The commonly growth factor as water, light and soil pH affect to fig trees like other plants. In *F. inspida* Willd., high light level and neutral soil pH result in better seed germination, faster growth and also higher survival rate of seedlings (Banack *et al.*, 2002).

Generally, the success of reproductive plant is not only in germination process but also in surviving of seedlings. Establishment in each species varies; some species take short but some species longer periods. Effects may be from biotic factors such as fungi, seed or seedling predators, or from the physical factors such as flood, aridity, humidity, light, etc (Sri-Ngernyuang *et al.*, 2007).

CHAPTER III

METHODOLOGY

3.1 TAXONOMIC STUDY

The preliminary survey was taken between 2005-2007 at Chiang Mai province in different kind of ecosystem and elevation. Monthly observation planned was used for investigating. Both fig trees and fig wasps were collected and work on taxonomic study in laboratory.

3.1.1 Fig tree

a. Collection

- Both vegetative and reproductive parts of fig trees were collected such as shoots, leaves, stipule and figs (syconium or inflorescence) throughout all season of the year from June 2005 to May 2007. Surveys base on geographical data in different habits and elevation distributed in Chiang Mai.
- Herbarium specimens were preserved both dry and in 70 % ethyl alcohol, especially fleshy syconium and the voucher specimens were collected at least 3 sets and deposit at Etnobotanical Research Section, Chiang Mai University, Chiang Mai.
- Plant information; habit, color, special characters, bract arrangement, syconium phenology and also date of collection have been recorded.
- Photography was taken.

b. Identification

- Specimens of figs were identified by observing morphological characters using Corner (1965), Berg (2005) and Zhekun and Gilert (2003).
- Plant collections were investigated and rechecked by comparison with the materials at the following herbaria; Forest herbarium, Bangkok (BKF), Chiang

Mai University Herbarium, Chiang Mai, Queen Sirikit Botanic Garden Herbarium, Chiang Mai (QBG), Xishuangbanna Tropical Botanic Garden (XTBG), China

c. Description

- Description of all species represented in site study.
- Taxonomic literatures were included.
- Occurrence in Thailand and their distribution taken from literature were cited.
- Ecological and phonological information of each species were described.
- Photographs and line drawing of each species were illustrated.

3.1.2 Fig wasp

a. Collection

- All of wasp immerged from syconium in each fig were collected.
- Insect specimens were preserved both dry and in 70 % ethyl alcohol.
- Insect information; host, color, size, dominant characters, and also date of collection have been recorded.
- Number of wasps in each species per syconium was measured.

b. Identification

- Morphological characters were used for verifying wasp to species level by using Bouček (1988), Weibes (1994) and Noort and Rasplus (2005b).
- Fig wasps specimens were rechecked by expert entomologist in fig wasps (Rasplus J.Y's, INRA-Centre de Biologie et de Gestion des Populations, France).

c. Description

- Description of all species of fig wasps pollinators which is represented in the study area.
- Occurrence in Thailand and their distribution taken from literature were cited.
- Photographs under the stereo microscope were taken.

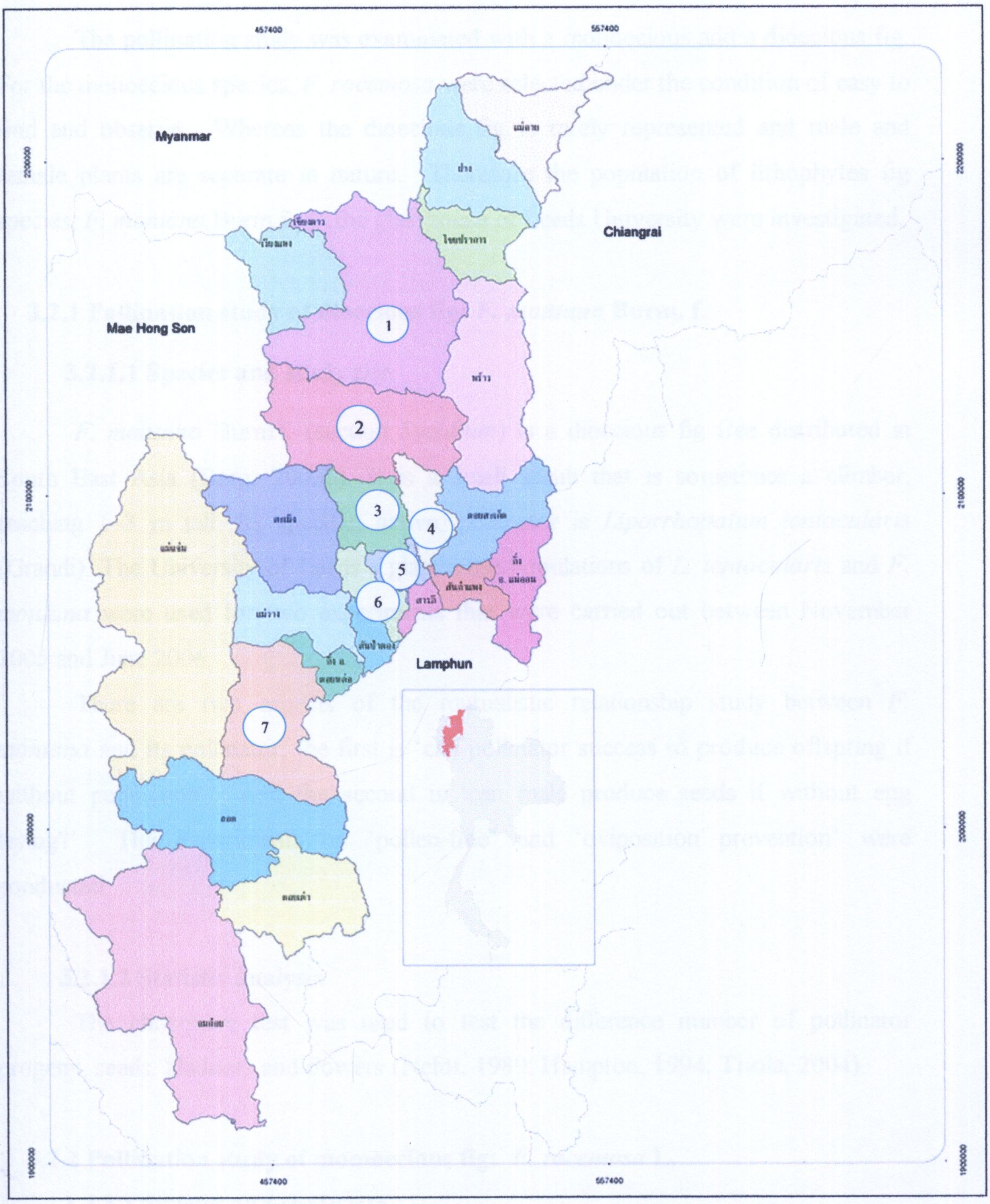


Figure 3.1 *Ficus* and fig wasps diversity's studies site, Chiang Mai, Thailand: 1. Chiang Dao, 2. Mae Tang, 3. Mae Rim, 4. Sansai, 5. Muang, 6. Hang Dong, 7. Chom Tong (http://www.chiangmai.go.th, 18 September 2007)

3.2 POLLINATION STUDY

The pollination study was examinated with a monoecious and a dioecious fig. For the monoecious species, *F. racemosa* were selected under the condition of easy to find and observe. Whereas the dioecious fig is rarely represented and male and female plants are separate in nature. Therefore the population of lithophytes fig species, *F. montana* Burm.f., in the glasshouse of Leeds University were investigated.

3.2.1 Pollination study of dioecious fig: *F. montana* Burm. f.

3.2.1.1 Species and study site

F. montana Burm.f. (section *Sycidium*) is a dioecious fig tree distributed in South East Asia (Berg, 2003b). It is a small shrub that is sometimes a climber, reaching 1–3 m tall. Its specific, active, pollinator is *Liporrhopalum tentacularis* (Grandi). The University of Leeds's glasshouse populations of *L. tentacularis* and *F. montana* were used for two experiments that were carried out between November 2005 and June 2006.

There are two aspects of the mutualistic relationship study between *F. montana* and its pollinator; the first is 'can pollinator success to produce offspring if without pollination? And the second is 'can male produce seeds if without egg laying?' The experiments on 'pollen-free' and 'oviposition prevention' were conducted.

3.2.1.2 Statistic analysis

The chi-square test was used to test the difference number of pollinator progeny, seeds, bladders and flowers (Nefdt, 1989; Hampton, 1994; Triola, 2004).

3.2.2 Pollination study of momoecious fig: *F. racemosa* L.

3.2.2.1 Species and study site

F. racemosa is a common fig tree with widely distribution in Southeast Asia (Zhang *et al.*, 2006). It is the one of few monoecious figs of subgenus *Sycomorus*

(Berg, 1989). The habit is a tree, reaching 25-40 m in height. It is a dominant species along the riverside of several rivers in Chiang Mai. Flowering and fruiting year-round represent. Its specific pollinator is *Ceratosolen fusciceps* Mayr. The population of *F. racemosa* in urban area of Chiang Mai were used for investigating that carried out from September 2006 to September 2007.

3.2.2.2 Field observation

Phenological censuses of *F. racemosa* were made around Chiang Mai, 10 figs tree were monitored during September 2006-September 2007. Censuses were made from each crop of all sampling tree as following issues;

1. Figs bearing in each crop
2. Leave covering in each crop
3. Fig size and flower number in each syconium
4. Style length in the B-C phase
5. The proportion of syconium containing pollinators, non pollinators and seeds

3.2.2.3 Laboratory study

Some figs were sampling to observe their six developing phase by picking 5 figs in each phase and study. The fig developing phase was described as follow (Yang *et al.*, 2002);

1. Early-floral phase, the syconium is seen as the size of a soybean seed, when the florets in the fig cavity are not visible.
2. Pre-female floral phase, when the syconium has just developed for 3-5 days, the miniature florets can be seen.
3. Female-floral phase, the female flower inside the syconium is in blossom and the fig wasp penetrates into the female syconium for pollination and the male ones for oviposition.
4. Interfloral phase, after fertilization took place in the female syconium, the fig embryo begin to develop and in the male syconium the gall flower are formed after oviposition by the foundress wasps and the larvae fully developed.

5. Male-floral phase, the flowers in the male syconium are open and become mature, and then carried by wasp.
6. Post-floral phase, seeds inside the female syconium ripened and soon female and male syconia both fell.

Fig specimens would be collected from the study areas during flowering stage. Plant specimens such as leaves shoots and syconium were taken to the laboratory, also their fig wasps. Twenty figs in early D phase were collected and kept in small containers that covered by fine cloth. All of wasps emerged were then dried for counting. Figs were taken to dissect in search of some remain wasps and to sample their seed production.

Both plant and insect specimens would be preserved in 70 % alcohol solution for future study. Morphological study of figs and their pollinators will be described by description and photography.

The fig wasps' specimens were classified by Bouček (1988) and Wiebes (1994).

3.2.2.4 Statistic analysis

The t-test was used to analyze quantitative measurements such as number of figs/tree, male pollinators/fig, female pollinators/fig, seeds/fig, total flowers/fig etc. (Nefdt, R.J.C. 1989; Hampton, 1994; Triola, 2004).

Figure 3.2 The species study of dioecious fig, *F. montana* in glasshouse

Figure 3.3 The species study of dioecious fig, *F. montana* in nature

Figure 3.4 *F. montana, a.* the syconium female fig, *b.* male fig

Figure 3.5 *F. racemosa* L., *a.* Tree with figs bearing, *b.* leaves, *c.* ripen figs

CHAPTER IV

TAXONOMIC STUDY OF SOME FIGS AND THEIR POLLINATORS

4.1 TAXONOMIC STUDY

29 taxa in 26 species were classified from six subgenera (Table 4.1). 2 species in *F. benjamina* L., 2 varieties in *F. racemosa* L. and *F. hispida* L. and 2 forms in *F. fistulosa* Reinw. ex. Bl. The largest group was 11 species in subgenus *Urostigma*, followed by 8 species of *Sycomorus*. *Ficus*, *Sycidium* and *Synoecia* each with 2 species and *Pharmacosycea* with 1 species.

Two varieties of *F. benjamina*; *F. benjamina* L. var. *benjamina* and *F. benjamina* L. var. *nuda* (Miq.) Barrett. The difference between them was the former had figs with glabrous and small size, 0.8-1.5 cm. in diameter, but the latter was about 1.8-2 cm. in diameter with pubescent figs. Their pollinator was the same, *Eupristina koningsbergeri* (Grandi) (Table 4.1) and non-pollinators were the insects in *Philotrypesis* and *Ormyrus* groups.

Another monoecious species with two varieties was *F. racemosa* consisted of *F. racemosa* L. var. *racemosa* and *F. racemosa* var. *miquell* (King) Corner. The former had branchlets, young leaves and figs with bent hair, whereas the latter had densely white pubescence. Its similar pollinator was *Ceratosolen fusciceps* Mayr. In addition, inside the fig, other fig wasps of 5 species were found. They were 2 species of *Apocrypta* and 3 species of *Platyneura* (*Apocryptophagus*).

For dioecious tree, *F. hispida* was the most generally disperse. There were two varieties in study site; *F. hispida* L.f. var. *hispida* and *F. hispida* var. *badiostrigosa* Corner. Their specific pollinator was *C. solmsi* Mayr. Its distribution was in the open area, sometimes near the stream and river. It occasionally appeared as pioneer species in the area of deforestation. Their ripen fruits also attracted to animals e.g. squirrels bats and insect-eating birds.

Fig wasps represented both pollinators and non pollinators. Eight genera of pollinators found consisted of *Blastophaga, Ceratosolen, Dolichoris, Eupristina,* *Liporrhopalum, Odontofroggatia, Platyscapa and Pleistodontes.* Non pollinating fig wasps comprised of *Acophila, Apocrypta, Camarothorax, Ormyrus, Otitesella, Philotrypesis, Platyneura* (*Apocryptophagus*) and *Sycoscapter* (Table 4.1).

Table 4.1 *Ficus* and their pollinators' checklist in Chiang Mai during June 2005-May 2007.

No	*Ficus* species	Pollinator	Other fig wasps
	Subgenus *Urostigma*		
1	*F. altissima* Bl.	*Eupristina altissima* Balakrishnan & Abdurahiman	Not seen
2	*F. benjamina* var. *benjamina* L.	*Eupristina koningsbergeri* (Grandi)	*Philotrypesis* sp. *Ormyrus* sp.
3	*F. benjamina* var. *nuda* (Miq.) Barrett.	*Eupristina koningsbergeri* (Grandi)	*Philotrypesis* sp. *Ormyrus* sp.
4	*F. curtipes* Corner	Not seen	Not seen
5	*F. drupacea* Thunb.	*Eupristina belgaumensis* Joseph	Not seen
6	*F. elastica* Roxb.	*Pleistodontes claviger* Mayr	Not seen
7	*F. lacor* Ham.	*Platyscapa* sp.	Not seen
8	*F. maclellandii* King	Not seen	Not seen
9	*F. microcarpa* L. f.	*Odontofroggatia galili* Wiebes	Not seen
10	*F. religiosa* L.	*Platyscapa quadraticeps* Mayr	Not seen
11	*F. rumphii* Bl.	Not seen	Not seen
12	*F. superba* Miq. var *japonica* Miq.	*Platyscapa* sp.	*Acophila* sp. *Camarothorax* sp. *Otitesella* sp. *Philotrypesis* sp. *Sycoscapter* sp.

Table 4.1 *Ficus* and their pollinators' checklist in Chiang Mai during June 2005-May 2007. (continued)

No	*Ficus* species	Pollinator	Other fig wasps
	Subgenus *Pharmacosycea*		
13	*F. callosa* Willd.	*Dolichoris malabarensis* Abdurahiman & Joseph	
	Subgenus *Sycomorus*		
14	*F. racemosa* L. var. *racemosa*	*Ceratosolen fusciceps* Mayr	*Apocrypta* sp.1 *Apocrypta* sp.2 *Platyneura* sp.1 *Platyneura* sp.2
15	*F. racemosa* L. var. *miquelli* (King) Corner	*Ceratosolen fusciceps* Mayr	*Apocrypta* sp.1 *Apocrypta* sp.2 *Platyneura* sp.1 *Platyneura* sp.2 *Platyneura* sp.3
16	*F. auriculata* Lour.	*Ceratosolen emarginatus* Mayr	*Philotrypesis longicaudata* Mayr *Platyneura* sp.
17	*F. fistulosa* Reinw ex. Bl. form1	*Ceratosolen constrictus* Mayr	Not seen
	F. fistulosa Reinw ex. Bl. form2	*Ceratosolen constrictus* Mayr	Not seen
18	*F. hispida* var. L.f. *hispida*	*Ceratosolen solmsi* Mayr	*Apocrypta bakeri* Joseph *Philotrypesis pilosa* Mayr

Table 4.1 *Ficus* and their pollinators' checklist in Chiang Mai during June 2005-May 2007. (continued)

No	*Ficus* species	Pollinator	Other fig wasps
	Subgenus *Sycomorus*		
19	*F. hispida* L.f. var. *badiostrigosa* Corner	*Ceratosolen solmsi* Mayr	*Apocrypta* sp. *Philotrypesis* sp.
20	*F. oligodon* Miq.	*Ceratosolen emarginatus* Mayr	*Apocrypta* sp.
21	*F. semicordata* Buch-Ham. ex. J. E. Sm.	*Ceratosolen gravelyi* (Grandi)	*Philotrypesis dunia* Joseph
22	*F. squamosa* Roxb.	*Ceratosolen* sp.	Not seen
23	*F. variegata* Bl.	*Ceratosolen appendiculatus* Mayr	Not seen
	Subgenus *Ficus*		
24	*F. ischnopoda* Miq.	*Blastophaga* sp.	Not seen
25	*F. hirta* Vahl	*Blastophaga javana* Mayr	*Philotrypesis* sp. *Sycoscapter* sp.
	Subgenus *Synoecia*		
26	*F. anserina* Corner	Not seen	Not seen
27	*F. pumila* L.	Not seen	Not seen
	Subgenus *Sycidium*		
28	*F. anastomosans* (Corner) Berg	*Liporrhopalum* sp.	*Philotrypesis* sp. *Sycoscapter* sp.
29	*F. subincisa* Buch.-Ham. ex. Smith	*Liporrhopalum* sp.	Not seen

4.2 CHARACTERS OF *FICUS* (Berg and Corner. 2005)

Tree, shrubs, or climbers, monoecious or (functionally) dioecious, often with aerial adventitious roots (hemi-epiphytes and root climbers), rarely with uncinate hairs, usually with waxy glandular spots on he lamina beneath and/or in the node if leafy twigs. **Leaves** spirally arranged, distichous, (sub) opposite (or subverticillate); stipule fully amplexicaul to lateral, mostly free. **Inflorescences** with an urceolate receptacle, entirely enclosing the flowers (even at anthesis), bisexual or (functionally) unisexual, pronouncedly protogynous, the orifice more or less tightly closed by bract; interfloral bracts present; staminate flowers with (2-) 3-5 (or more) scarious tepals, these free in shape. **Fruit** a drupelet or an achene. **Seed** with endosperm, embryo (almost) straight with flat and equal or ± curved with conduplicate cotyledon.

KEY TO SUBGENERA OF *FICUS*

1a. Plants monoecious, the figs containing staminate flowers and pistillate flowers with different style length; leaves usually in spiral, rarely subdistichous or subopposite; lamina rare scabrous..(2)

b. Plants (gyno) dioecious, the figs containing either staminate flowers and pistillate flowers with short style or only pistillate flowers with long style (or also neuter flowers); leaves often distichous or (sub) opposite......................................(4)

2a. Figs without interfloral bracts; staminate flowers near the ostiole and subtended and enveloped by 2 bracteoles. ....***Subg. Sycomorus***

b. Figs with interfloral bracts; staminate flowers mostly scattered among the pistillate one and without bracteoles. ....(3)

3a. Waxy gland one, at the base of the midrib beneath; aerial adventitious roots usually present; stamen usually 1; stigma usually 1, usually distinctly papillate. ....***Subg. Urostigma***

b. Waxy gland two, in the axils of the basal lateral veins beneath or absent; aerial roots absent; stamens 1 or 2; stigma usually 2, without distinctly papillate. ....***Subg. Pharmacosycea***

4a. Stipule often not fully amplexicual; lamina often asymmetric; bracts mostly scattered on the peduncle and not 3 in a whorl as basal bracts; pistillode (or pistil) always present in the staminate flower.................................***Subg. Sycidium***

b. Stipule nearly always fully amplexicual; lamina symmetric or asymmetric; basal bracts 3, in a whorl, sometime basal or lateral bracts not distinguishable; pistillode rarely present...(5)

5a. Root-climbers usually with pronounced leaf dimorphy.
....***Subg. Synoecia***

b. Tree or shrubs without aerial roots and leaf dimorphy.............................(6)

6a. Staminate flowers near the ostiole and mostly subtended by bracteoles; figs often cauliflorous or flagelliflorous; lateral bracts often present; lamina often asymmetric; in dried material the nodes of leafy twigs often thicker than the internodes and the lamina with lead-colored spots above.
....***Subg. Sycomorus***

b. Staminate flowers scattered among the pistillate ones or near the ostiole, not subtended by bracteoles; figs mostly axillary or just below the leaves; lamina symmetric; in dried material the nodes of leafy twigs almost as thick as the internodes and lead-colored spots absent on the lamina above.
....***Subg. Ficus***

4.3 CHARACTERS OF FIG WASPS

4.3.1 Super family Chalcidoidae

As the previous knowledge, all of 'fig wasps' are the insects in family Agaonidae and Chalcididae, super family Chalcidoidae, Order Hymenoptera (Bouček, 1988). The significant characters to identify fig wasp are the main of their morphology such as antenna, head, wing, thorax, gaster, legs and ovipositor. The general Chalcidoidae morphologies were explained by Pitkin (2004) in figure 4.1 to 4.8

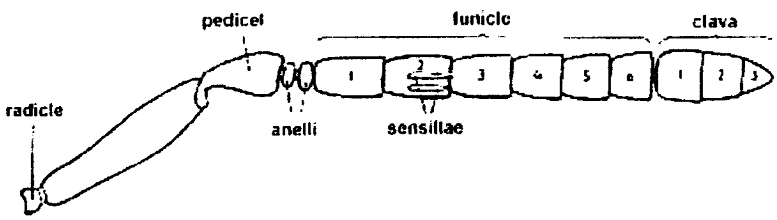


Figure 4.1 Characters of Chalcidoidae; Antenna (after Pitkin, 2004)

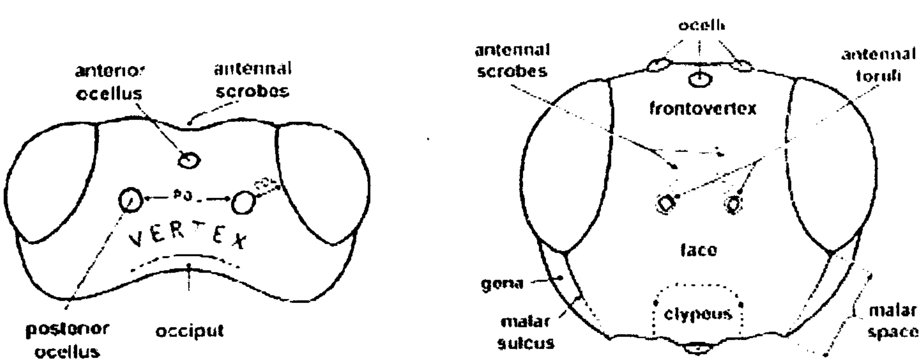


Figure 4.2 Characters of Chalcidoidae; Head (after Pitkin, 2004)

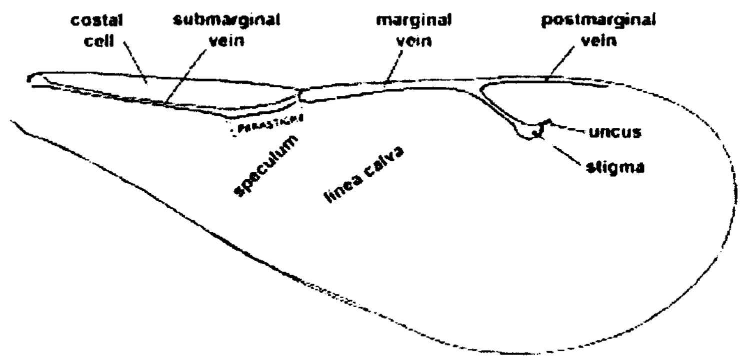


Figure 4.3 Characters of Chalcidoidae; Fore wing (after Pitkin, 2004)

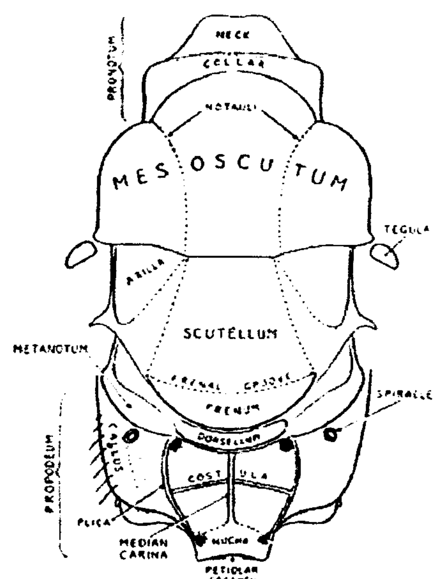


Figure 4.4 Characters of Chalcidoidae; Thorax -dorsal view (after Pitkin, 2004)

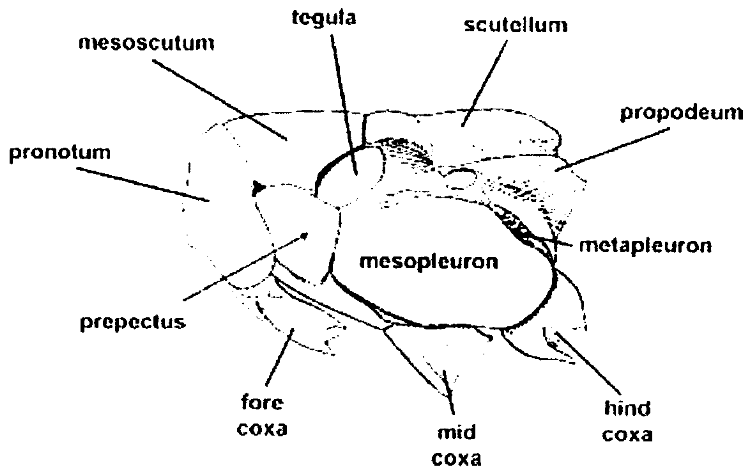


Figure 4.5 Characters of Chalcidoidae; Thorax -side view (after Pitkin, 2004)

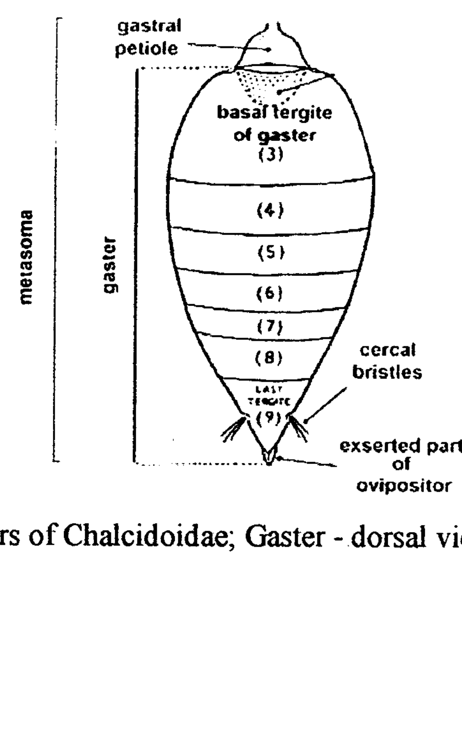


Figure 4.6 Characters of Chalcidoidae; Gaster - dorsal view (after Pitkin, 2004)

4.3.2 Family Agaonidae

Pitkin (2004) reported that this family currently includes 76 genera and 757 species placed in 6 subfamilies as follows: Agaoninae (20/358), Epichrysomallinae (14/40), Otitesellinae (15/79), Sycoecinae (6/67), Sycophaginae (7/59), Sycoryctinae (11/151), unplaced (3/3). The first subfamily is known as pollinator function, but the others are may be parasitoids or gall-formers. Hence at least 20 genera and 358 species of pollinators were published, however more than half of them still undiscovered (if refer to 1,000 species of figs).

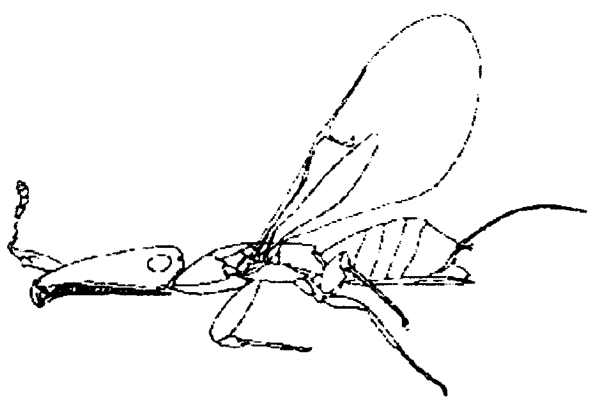
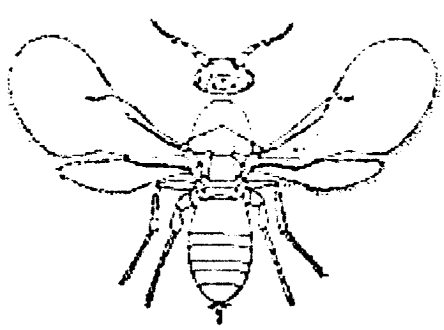
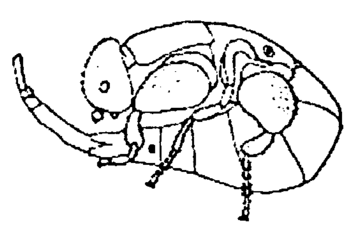


Figure 4.7 Female Agaoninae pollinator; *Pleistodontes* sp. (after Pitkin, 2004)



female



male

Blastophaga psenes

Figure 4.8 Illustration of male and female pollinators in *Blastophaga* (after Pitkin, 2004)

Key to genera of subfamily Agaoninae (Wiebes, 1994)

1. The female head is slightly too strong longer than wide. The third antennal segment is rather simple, in that the produced apex, if at all prominent, is not separate from the main part of the segment; the pedicel has no axial spines. The mandibular appendage is truly appended to the mandible; it has ventral lamellae, but mostly rows of small teeth. All male tarsi are pentamerous and the pronotum does not have anterolateral expansions..*Pleistodontes*
   - The female head is usually not distinctly elongate. The third antennal segment has a separation between the main part and the produce apex, which itself may be divided; the pedicel has axial spines. The mandibular appendage is fuse with the body of the mandibular; it bears ventral lamellae. The male fore tarsus is bimerous, the pronotum has characteristic antero-lateral expansions *Waterstoniella*..(2)
2. In the female, the spiracle of the eight urotergite has large, elongate peritremata, and the wing-venation is complete. The male antennae are slender, placed in deep channels, which are interiorly separated by a triangular raised area bearing usually three (rarely two) sharp frontal lobe, and the thorax (the pronotum in particular) is elongate the mid tarsi are usually pentamerous............................*Ceratosolen*
   - The spiracles are smaller and mostly subcircular- if they are larger and oval, the wing-venation is obsolete beyond the marginal vein (*Eupristina*). The male antennae are usually shorter and more clavate – if they resemble those of *Ceratosolen*, the thorax is more robust and the mid tarsi are oligomerous ....(3)
3. The ovipositor valves of the female are as long as the gaster, or longer. The antenna consists of eleven segments. The male genitalia are usually simple (not in *Dolichoris*..(4)
   - The ovipositor-vales are shorter than the gaster, mostly half as long or shorter, but exceptionally three-quarters of the length of the gaster. Usually the male gentalia bear cerci with claws ....(8)
4. The venation of the female fore wing is reduced: it is obsolete beyond the marginal vein. The male thorax is tapering caudad.......................................*Eupristina*

- The venation of female fore wing is more complete, and the male thorax is not tapering caudad..(5)

5. The female antenna is strongly clavate...*Deilagaon*
- The female antenna, if at all, is not that strongly clavate..........................(6)

6. The median ocillous of the female is reduced. The maxilla is simple, all male tarsi are pentamerous. The pronotum usually is expanded fronted. ....*Waterstoniella*
- The female has all ocilli normally developed. The maxilla has a bacilliform process. The male fore tarsi usually are bimerous......................................(7)

7. The spine of the female hypopygium bears one or two row(s) of hyaline setae the male metanotum is visible dorsally as two ear-like plates. The genitalia have (sometimes indistinct) claspers with claws....................................*Dolochoris*
- The spine of the female hypopygium does not have transverse row(s) of hyaline setae. The male metanotum and the propodeum are completely separated, or only laterally. The genitalia are simple.. *Platyscapa*

8. The female fore tibia bear four or more dorso-apical teeth, and that of the male, seven or more...*Kradibia*
- The fore tibia of the female bear two or three dorsal-apical teeth, and that of the male (two)-tree or four (-five)..(9)

9. The female antenna has ten segments..(10)
- The female antenna has eleven segments...(11)

10. The wing-venation is partly or quite indistinct- if it is distinct and complete, then the antennal segments are four or more times as long as wide. The male mid tarsus has two or three segments...*Liporrhopalum*
- The wing-venation is distinct, and the antennal segment are little longer than wide. The male mid tarsus is atrophied...*Weibesia*

11. The female mesoscutum has a longitudinal groove (fig. 2, m) – if tis is not distinct, the fore tibia bear four dorsal-apical teeth (no. 96, *W. nuda*) or three, but then the hypopygial spine does not bear a row of hyaline setae.......... *Weibesia*
- The female mesoscutum is entire; if the fore tibia bears three dorsal-apical teeth, the hypopygial spine bears a transverse row of hyaline setae ....*Blastophaga*

4.4 TAXONOMIC STUDY OF *FICUS* L.

Specimens of fig trees that represented in Chiang Mai were identified to twenty-six species. Their characters were described and their pollinators were identified. The flowering and fruiting crops, ecology and distribution were indicated.

Monoecious Figs

Subgenus ***Urostigma***

1. *Ficus altissima* Bl.

กร่าง (Krang) (Figure 4.9, 4.36)

Trees, 25-30 m tall; branchlets green, ca. 1 cm thick, pubescent. Stipules 2-3 cm long, thick leathery, with silky hairs. **Leaf**: blade broadly ovate to broadly ovate-elliptic, 10-19 × 8-11 cm, thick leathery, glabrous; base broadly cuneate; margin entire; apex obtuse; basal lateral veins long; secondary veins 5-7 on each side of midvein; petiole 2-5 cm. **Figs**: axillary on leafy branchlets, paired, red or yellow when mature, ellipsoid-ovoid, 1.7-2.8 cm in diam., pubescent when very young, glabrous when mature, sessile; involucral bracts hood-like, covering young fig, scar ringlike. Male, gall, and female flowers within same fig. **Male flowers**: scattered; perianth 4, transparent, membranous; stamen 1. **Gall flowers**: perianth 4; style subapical. **Female flowers**: sessile; perianth 4; style elongated. **Fruit**: achenes, ovoid-reniform, 1x2 mm.

Flowering: March-April **Fruiting:** May-July

Ecology: generally occur in lowland, altitude 310-1,000 m

Pollinator: *Eupristina altissima* Balakrishnan & Abdurahiman

2. *Ficus benjamina* L. var. *benjamina*

ไทรย้อยใบแหลม (Sai yoi bai laem, Golden fig) (Figure 4.10, 4.36)

Trees, up to 20 m tall, crown wide; bark smooth; main branches producing aerial roots which can develop into new trunks; branchlets pendulous, glabrous; stipules caducous, lanceolate, 0.6-1.5 cm, membranous, glabrous. **Leaf**: blade ovate to broadly elliptic, 4-8 × 2-4 cm, leathery, glabrous; base rounded to cuneate; margin entire; apex shortly acuminate, secondary veins 8-10 on each side of midvein, parallel, petiole 1-2 cm **Figs**: axillary on leafy branchlets, paired or solitary, purple, red, or yellow when mature, globose to subglobose, 0.8-1.5 cm in diam., glabrous, sessile; involucral bracts inconspicuous, triangular-ovate, glabrous, persistent. Male, gall, and female flowers within same fig. **Male flowers**: few, shortly pedicellate; perianth 3 or 4, broadly ovate; stamen 1; filament rather long. **Gall flowers**: many, perianth 3, 4 or 5, narrowly, spatulate; ovary ovoid, smooth; style lateral, short. **Female flowers**: sessile or pedicellate; perianth 3, shortly spatulate; style ± lateral, short; stigma enlarged. **Fruit:** achenes, ovoid-reniform, 1x1 mm, shorter than persistent style.

Flowering: 3 times; August, November, March **Fruiting:** September, October, May

Ecology: widespread, moist mixed forest, 310-800 m

Pollinator: *Eupristina koningsbergeri* (Grandi)

3. *Ficus benjamina var. nuda* (Miq.) Barrett.

ไทรย้อยใบแหลม (Sai yoi bai laem, Golden fig) (Figure 4.10)

The different from var. *benjamina* is the fig size 1.8-2 cm in diam. and pubescent. Pollinator: *Eupristina koningsbergeri* (Grandi)

4. *Ficus curtipes* Corner

ไทรหิน (Sai hin) (Figure 4.11)

Trees, 5-10 m tall; epiphytic when young; stems often basally many branched; Bark pale grayish, smooth; branchlets green, 5-8 mm in diam., glabrous. Stipules lanceolate to ovate lanceolate, 1-2 cm. **Leaf**: blade narrowly elliptic to ovate-elliptic, 12-18 × 5-6 cm, thick leathery; base cuneate; margin entire; apex acute; basal lateral veins short; secondary veins 8-12 on each side of midvein, inconspicuous on both surfaces; petiole robust, 1.5-2 cm. **Figs**: axillary on leafy branchlets; paired; dark red to purplish red when mature; globose to sub-globose; 1-1.5 cm in diam.; sessile; involucral bracts green, broadly ovate, 3-4 mm. Male, gall, and female flowers within same fig. **Male flowers**: pedicellate; perianth 3; lanceolate; stamen 1. **Gall flowers**: sessile or pedicellate; perianth 4; ovary white; style subapical. **Female flowers**:

sessile; style subapical, persistent, as long as achene; stigma funnelform. **Fruit**: achenes, ovoid, 1x2 mm.

Flowering: November-December **Fruiting:** December-January

Ecology: moist area, near the stream, 350-850 m

Pollinator: not seen in study areas

5. *Ficus drupacea* Thunb.

ลุงขน (Lung khon, Mysore fig) (Figure 4.12, 4.36)

Trees, 10-15 m tall; bark grayish white; branches without aerial roots; branchlets 5-9 mm in diam., densely yellowish brown woolly. Stipules yellowish brown, lanceolate, 2-3 cm, membranous, with thick hairs. **Leaf**: blade narrowly elliptic to obovate-elliptic, 15-18 × 5-9 cm, leathery, glabrous or pubescent; base rounded, ± cordate, or ± auriculate; margin entire or slightly undulate; apex acute; basal lateral veins 2-4; secondary veins 8-11 on each side of midvein; tertiary veins reticulate. **Figs**: axillary on leafy branchlets, paired, reddish orange to red and with scattered white spots, oblong, pillow-shaped, or conic-ellipsoid, 1.5-2.5 × 1-1.5(-2) cm, glabrous or densely covered with brownish yellow long hairs, inside with few or no bristles; involucral bracts orbicular to ovate lanceolate; margin ciliate. Male, gall, and female flowers within same fig. **Male flowers**: long-pedicellate; perianth 3-4, broadly ovate; stamen 1; filament short and thick; anther narrowly ellipsoid. **Gall flowers**: pedicellate; perianth connate, apically 3- or 4- lobed; ovary globose. **Female flowers**: perianth 3, white, broadly lanceolate. **Fruit:** achenes, globose.

Flowering: January-February **Fruiting:** February-March

Ecology: open area, in deciduous forest near the stream, 320-700 m

Pollinator: *Eupristina belgaumensis* Joseph

6. *Ficus elastica* Roxb.

ยางอินเดีย (Indian rubber fig) (Figure 4.13, 4.36)

Trees, 20-30 m tall; epiphytic when young; bark smooth; Stipules dark red, ca. 10 cm, membranous; scar conspicuous. **Leaf**: blade oblong to elliptic, 8-30 × 7-10 cm, thickly leathery; base broadly cuneate; margin entire; apex acute; secondary veins many, closely parallel, inconspicuous; petiole 2-5 cm. **Figs:** axillary on leaf branchlets, paired or solitary, yellowish green, ovoid-ellipsoid, ca. 10 × 5-8 mm, subsessile; involucral bracts hoodlike, caduceus; scar conspicuous. Male, gall, and female flowers within same fig. **Male flowers**: scattered among other flowers; pedicellate; perianth 4, ovate; stamen 1; filament absent; anther ovoid-ellipsoid. **Gall flowers**: sessile; perianth 4; ovary ovoid, smooth; style subapical, curved. **Female flowers**: sessile; style persistent, long; stigma enlarged, ± capitate. **Fruit**: achenes, ovoid, tuberculate, 1x1 mm.

Flowering: December-January **Fruiting:** January-February

Ecology: plant in town, often cultivated, 310-500 m

Pollinator: *Pleistodontes claviger* Mayr

7. ***Ficus lacor* Buch. Ham.**

ผักเฮือด (Phak hueat) (Figure 4.14)

Tree. 12-20 m tall; bark gray, smooth; branchlets strong. Stipules pink, ca. 8-10 cm, membranous; scar conspicuous. **Leaf**: blade oblong to elliptic or ovate elliptic, purple-red when young, glabrous, 7-10 x 12-16 cm; base widely cuneate; apex acuminate; margin entire; lateral nerves 7-11 pairs; petiole 4-8 cm. **Fig** globose, ca. 10 mm wide, pale pink color with tomentose; sessile or shortly; pedunculate; basal bracts covering only the base of the body. Male, gall, and female flowers within same fig. **Male flowers**: scattered among other flowers; pedicellate; perianth 4, generally narrow; stamen 1. **Gall flowers**: sessile; perianth 4; ovary ovoid, smooth; style subapical, curved. **Female flowers**: sessile; perianth 4; style persistent, long; stigma enlarged, capitate. **Fruit**: achenes, ovoid, tuberculate, 1x1 mm.

Flowering: January-February **Fruiting:** February-March

Ecology: open area, in the village, 310-600 m

Pollinator: *Platyscapa* sp.

8. ***Ficus maclellandii*** **King**

ไทรย้อย (Sai yoi) (Figure 4.15, 4.36)

Trees, 15-20 m tall; bark smooth; branchlets dark brown, ribbed and densely tuberculate. Stipules lanceolate, 0.4-1 cm, sparsely appressed pilose. **Leaf**: blade oblong to ovate-elliptic, 8-13 × 4-6 cm, leathery, glabrous but occasionally pubescent when young; base rounded to cuneate; margin entire; apex acuminate to mucronate; basal lateral veins 2, prominent; secondary veins 10-13 on each side of midvein, conspicuous on both surfaces, and with cystoliths between veins; petiole 1.3-1.7 cm glabrous. **Figs**: axillary on leafy branchlets, paired, purplish red when mature, globose to conic, slightly flat, 6-8 mm in diam.; sessile; involucral bracts 2 or 3, ovate, 2.3 mm; unequal in size. Male, gall, and female flowers within same fig. **Male flowers**: few, near apical pore; sessile; perianth 4, short, narrow lanceolate; stamen 1. **Gall flowers**: sessile; perianth 4, lanceolate, ovary globose. **Female flowers**: pedicelate; perianth 4, lanceolate, short, ovary ovoid; style subapical. **Fruit:** achenes, ovoid, 1x1 mm.

Flowering: May-June, November-December **Fruiting:** June, December

Ecology: open area, 310-800 m, growing in the city

Pollinator: not seen in study areas

9. ***Ficus microcarpa*** **L. f.**

ไทรย้อยใบทู่ (Sai yoi bai thu) (Figure 4.16, 4.37)

Trees, 15-25 m tall, crown wide; bark dark gray; branches producing rust-colored aerial roots when old; stipules lanceolate, ca. 0.8 cm. **Leaf**: blade elliptic to obovate, 4-8 × 3-4 cm, leathery, leaf dark brown when dry; base rounded cuneate; margin entire; apex obtuse; basal lateral veins long; secondary veins 3-10 on each side of midvein; petiole 5-10 mm. **Figs**: axillary on leafy branchlets or on leafless older branchlets, paired, yellow to slightly red when mature, depressed globose, 6-8 mm in diam., inside with a few short bristles among flowers, sessile; involucral bracts broadly ovate, persistent. Male, gall, and female flowers within a same fig. **Male flowers**: scattered; sessile or pedicellate; filament as long as anther. **Gall and Female**

flowers: perianth 3, broadly ovate, membranous; style lateral; stigma short, clavate. **Fruit**: achenes, ovoid, 1x1 mm.

Flowering: April-June, August-September **Fruiting:** May-July, October

Ecology: open area, near the river, often cultivated in the city, 310-700 m

Pollinator: *Odontofroggatia galili* Wiebes

10. ***Ficus religiosa*** **L.**

โพศรีมหาโพ (Pho si maha pho, Sacred fig tree) (Figure 4.17, 4.37)

Trees, 15-25 m tall, banyans, strangling figs with adventitious roots, epiphytic when young, crown wide when mature; bark gray, smooth or longitudinally; branchlets grayish brown, sparsely pubescent when young. Stipules ovate, small, apex acute. **Leaf**: blade triangular-ovate, 9-17 × 8-12 cm, leathery; base broadly cuneate to cordate; margin entire or undulate; apex acute to acuminate; basal lateral veins 2; secondary veins 5-7 on each side of midvein; petiole slender, at least as long as half of leaf blade. **Figs**: axillary on leafy branchlets, paired or solitary, red when mature, globose to depressed globose, 1-1.5 cm in diam., smooth; peduncle 4-9 mm; involucral bracts ovate. Male, gall, and female flowers within same fig. **Male flowers**: few, near apical pore; sessile; perianth 2- or 3-lobed; margin revolute; stamen 1; filament short. **Gall flowers**: subsessile; perianth 3- 4, short, ovary oblong, smooth; style short; stigma enlarged, 2-lobed. **Female flowers**: sessile; perianth 4, short, narrow lanceolate; ovary oblong, smooth; style and stigma short. **Fruit**: achenes, oblong, 1x1 mm.

Flowering: March-April **Fruiting:** May-June

Ecology: open area, both in town and in deciduous forest, 310-750 m

Pollinator: *Platyscapa quadraticeps* Mayr

11. ***Ficus rumphii*** **Bl.**

โพขี้นก (Pho khi nok) (Figure 4.18, 4.37)

Trees, 15 m tall; usually epiphytic; bark gray, wrinkled when dry. Stipules caducous, ovate-lanceolate, 1.5-2.5 cm; scar conspicuous, glabrous. **Leaf**: leaf blade cordate to ovate-cordate, 6-13 × 6-11 cm, leathery, glabrous; base cordate to broadly cuneate; apex acute to acuminate; basal lateral veins 4; secondary veins 5 or 6 on each side of midvein; petiole 6-8 cm. **Figs**: axillary on leafy branchlets, paired or in small clusters on leafless older branchlets, with dark spots when young, dark purple when mature, globose, 1-1.5 cm in diam., sessile; involucral bracts orbicular, small; apical bracts navel-like. Male, gall, and female flowers within same fig. **Male flowers**: few, scattered among other flowers; sessile; perianth 3, spatulate; stamen 1; filament as long as anther. **Gall flowers**: sessile; perianth 3, lanceolate, shorter than ovary. **Female flowers**: perianth 4, narrow lanceolate, shorter than ovary; ovary white, ovoid, smooth; style persistent; stigma clavate. **Fruit:** achenes thin, tuberculate, 1x1 mm.

Flowering: July-August, September **Fruiting:** August-September, October

Ecology: open area, 100-700 m

Pollinator: not seen in study areas

12. ***Ficus superba*** **var.** ***japonica*** **Miq.**

ไกร, เลียบ (Liap) (Figure 4.19, 4.37)

Trees, without aerial roots, bark brown. Stipules 5-10 cm long and leafy on the opening shoots, closely puberulous to subglabrous, pink. **Leaf**: leaf spirally arranged, glabrous, 5-8 x 9-15 cm, elliptic to oblong-elliptic; base truncate-subcordate to rounded, thinly coriaceous; lateral nerves 7-9(-10) pairs; basal nerves 2-3 pairs; petiole 4-16 cm. **Figs**: ramiflorous in pairs and in small clusters on woody on the twigs and branches, rarely in the leaf-axils; fig-body 7-11 mm wide, ripening white to pink, purple and black; peduncle 2-15 mm long. **Male flowers**: ostiolar in 2-3 rings; sessile; perianth bifid, membranous. **Gall-flowers**: sessile or with a short pedicel; perianth 3-4, free, reddish; ovary red-brown. **Female Flowers**: as the gall-flowers, but subsessile; style long, internal bristles none or few. **Fruit**: achene, subglobose, 1x1 mm.

Flowering: January-February **Fruiting:** February-March

Ecology: deciduous forest, in the village, 320-500 m

Pollinator: *Platyscapa* sp.

Subgenus ***Pharmacosycea***

13. ***Ficus callosa*** **Willd.**

มะเดื่อกวาง (Ma duea kwang) (Figure 4.20, 4.37)

Trees, 25-35 m tall; bark gray to pale gray, hard; branchlets wrinkled when dry. Stipules ovate-lanceolate, 1-1.8 cm, pubescent. **Leaf**: blade broadly elliptic, 15-30 × 8-20 cm, leathery, scabrid on lower surface; base rounded to broadly cuneate; margin entire; apex obtuse or mucronate; secondary veins 8-11 on each side of midvein, prominent on both surfaces; petiole 3-9 cm. **Figs**: axillary on normal leafy stem, paired or solitary, yellow when mature; pear-shaped-ellipsoid, 1.2-2.5 × 1-1.5 cm, pubescent; base attenuate into a 1 cm stalk; apical pore flat; peduncle 1-1.2 cm; involucral bracts lanceolate-ovate, ca. 2 mm. Male, gall, and female flowers within same fig. **Male flowers**: near apical pore or scattered; subsessile; perianth 3-5, spatulate; stamen 1, filaments long. **Gall flowers**: subsessile; perianth 4, broadly lanceolate; stigma short. **Female flowers**: subsessile; perianth deeply 4-lobed, broadly lanceolate; style subapical, long and thin; stigma deeply 2-branched. **Fruit**: achenes, obovoid, 1x2 mm.

Flowering: August, October **Fruiting:** September, November

Ecology: open area, cultivated in town, 310-500 m

Pollinator: *Dolichoris malabarensis* Abdurahiman & Joseph

Subgenus ***Sycomorus***

14. ***Ficus racemosa*** **L. var.** ***racemosa***

มะเดื่ออุทุมพร (Ma dduea utum phon) (Figure 4.21)

Trees, 25-30 m tall; monoecious; bark grayish brown, smooth. Stipules ovate-lanceolate, 1.5-2 cm. **Leaf**: ovate-lanceolate, 5-8 x 10-15 cm, glabrous; base cuneate; margin entire; apex acute, young leaf blades and figs with bent hairs. Petiole 2-6 cm. **Figs**: paired or cluster on leafy branchlets, reddish orange when mature; pear-shaped, 2-5 cm in diam.; basally attenuated into a stalk; peduncle ca. 1 cm; involucral bracts triangular-ovate. Male, gall, and female flowers within same fig. **Male flowers**: near apical pore; subsessile; perianth 3 or 4, spatulate; stamens 2. **Gall flower:** both short and long pedicel present; perianth broadly with 3 or 4 toothed; style lateral. **Female**

flowers: short pedicel; perianth broadly; apex 3 or 4 toothed; style lateral and long; stigma clavate. **Fruit**: achene, subglobse, 1x2 mm.

Flowering: year-round **Fruiting:** year-round

Ecology: riverside, along the stream, moist forest, 310-1,200 m

Pollinator: *Ceratosolen fusciceps* Mayr (Figure 4.42, 4.44)

15. ***Ficus racemosa*** **L. var.** ***miquelli*** **(King) Corner**

มะเดื่ออุทุมพร (Ma dduea utum phon) (Figure 4.21)

The different from var. *racemosa* is branchlets, young leaf blades, and figs densely covered with straight white pubescence.

Dioecious Figs

16. ***Ficus auriculata*** **Lour.**

เดื่อหว้า (Duea wa) (Figure 4.22, 4.38, 4.41)

Trees, 4-10 m tall, crown elongated and wide; dioecious; bark grayish brown, rough; branchlets reddish brown, 1-1.5 cm thick; leafless in middle of stem, pubescent. Stipules reddish purple, triangular-ovate, 1.5-2 cm, adaxially shortly pubescent. **Leaf**: alternate; leaf blade broadly ovate-cordate, 15-55 × 15-27 cm, glabrous or puberulent on midvein or secondary veins; base cordate to occasionally rounded; margin dentate; apex obtuse; basal lateral veins 4-6; secondary veins 3 or 4 on each side of midvein; petiole thick, 5-8 cm. **Figs**: on specialized leafless branchlets at base of trunk and main branches, reddish brown, pear-shaped, depressed globose, or top-shaped, with 8-12 conspicuous longitudinal ridges, 3-6 cm in diam., shortly pubescent when young, glabrescent when mature; peduncle 2-6 cm, thick, pubescent; involucral bracts triangular-ovate; apical bracts in 4 or 5 rows, broadly triangular-ovate, imbricate, rosulate. **Male flowers**: sessile; perianth 3, transparent, broadly spatulate, thinly membranous; stamens 2; filaments long; anthers ovoid. **Gall flowers**: perianth 3, apically free, covering ovary; style lateral; stigma enlarged. **Female flowers**: pedicellate or sessile; calyx lobes 3; ovary ovoid; style lateral. **Fruit**: achene, subglobose, 1x2 mm.

Flowering: 2 times; March, August **Fruiting:** 2 times; May, October

Ecology: forests in moist valleys, 600-2,000 m

Pollinator: *Ceratosolen emarginatus* Mayr

17. ***Ficus fistulosa*** **Reinw. ex Bl.**

ชิ้งแดง (Ching deang) form1 (Figure 4.23, 4.38, 4.41)

Small trees, bark dark brown; branchlets hispid. Stipules ovate-lanceolate, 1-2 cm. **Leaf**: alternate; leaf blade obovate to oblong, 10-20 × 4-8 cm, papery; base obliquely cuneate to rounded; margin entire or coarsely serrate; apex mucronate; basal lateral veins short; secondary veins 6-9 on each side of midvein; petiole 1.5-4 cm. **Figs**: on short branchlets on main branches, reddish orange or yellow when mature, globose, 1.5-2 × 1.5.-2.2 cm, subglabrous, smooth, apical pore not open; peduncle 0.8-2.4 cm. **Male flowers**: few, near apical pore; pedicellate; perianth 3 or 4; stamen 1; filament short. **Gall flowers**: sessile; perianth very short or absent; ovary obovate, smooth; style lateral, thin; stigma enlarged. **Female flowers**: pedicellate; perianth absent; style persistent, long, clavate. **Fruit:** achenes obliquely cubic, with small tubercles, 1x1 mm.

Flowering: February-April **Fruiting:** March-July

Ecology: forests along streams, 310-1,200 m

Pollinator: *Ceratosolen constrictus* Mayr

Ficus fistulosa **Reinw. ex Bl.**

ชิ้งขาว (Ching Khao) form2 (Figure 4.24)

Small trees, bark dark brown; branchlets hispid. Stipules ovate-lanceolate, 1-2 cm. **Leaf**: alternate; leaf blade obovate to oblong, 10-20 × 4-8 cm, papery; base obliquely cuneate to rounded; margin entire or coarsely serrate; apex mucronate; basal lateral veins short; secondary veins 6-9 on each side of midvein; petiole 1.5-4 cm. **Figs**: on short branchlets on main branches, reddish orange or yellow when mature, globose, 1.5-2 × 1.5.-2.2 cm, subglabrous, smooth; apical pore not open; peduncle 0.8-2.4 cm. **Male flowers**: few; near apical pore; short pedicel; perianth 3 or 4, enclosing; stamen 2; filament short. **Gall flowers**: sessile; perianth very short; ovary obovate, smooth; style lateral, thin; stigma enlarged. **Female flowers**: perianth tubular, enclosing base of pedicel; style persistent, long, clavate. **Fruit:** achenes obliquely cubic, with small tubercles, 1x1.5 mm.

Flowering: May-July **Fruiting:** July-August

Ecology: forests along streams, moist area, 310-1,200 m

Pollinator: *Ceratosolen constrictus* Mayr

18. *Ficus hispida* L. f. var. *hispida*

มะเดื่อปล้อง (Ma duea plong) (Figure 4.25)

Shrubs or small trees, coarsely hairy, dioecious. Stipules usually 4 and decussate on leafless fruiting; branchlets, ovate-lanceolate. **Leaf**: opposite, with short thick hairs; blade ovate, oblong, or obovate-oblong, 10-25 × 5-10 cm, thickly papery; hispid on both surface; base rounded to cuneate; margin entire or toothed; apex acute; secondary veins 6-9 on each side of midvein; petiole 1-6 cm. **Figs**: axillary on fascicle from main stem, branch or leaf axile, covered by pale hairs, solitary or paired, yellow or red when mature, top-shaped, 1-3 cm in diam., with short scattered hairs; pedunculate; involucre bracts present; lateral bracts sometimes present. **Male flowers**: many, near apical pore, subsessile; perianth 3, broadly lanceolate, thinly membranous; stamen 1; filament long. **Gall flowers**: pedicellate; perianth absent; style subapical, short, thick. **Female flowers**: perianth absent; style lateral, long, hairs; ovary subglobose. **Fruit**: achene, subglobose, 1x2 mm.

Flowering: year-round **Fruiting:** year-round

Ecology: along streams, or moist soil areas, 310-1,500 m

Pollinator: *Ceratosolen solmsi* Mayr (Figure 4.42)

19. *Ficus hispida* var. *badiostrigosa* Corner

มะเดื่อปล้อง (Ma duea plong) (Figure 4.25)

The different from var. *hispida* was figs on stolon which creeping on the ground or under ground (geocarpic figs), covered with dark brown hairs.

Flowering: year-round **Fruiting:** year-round

Ecology: along streams, or moist soil areas, in the village, 310-1,500 m

Pollinator: *Ceratosolen solmsi* Mayr

20. ***Ficus oligodon*** **Miq.**

เดื่อหลวง (Duea luang) (Figure 4.26)

Trees, 5-10 m tall; crown wide; dioecious; bark gray, smooth; branchlets sparsely pubescent. Stipules caducous, ovate-lanceolate, 1-1.5 cm, glabrous or puberulent. **Leaf**: alternate; blade obovate-elliptic to elliptic, 12-25 × 6-23 cm, papery; base shallowly cordate to broadly cuneate; margin irregularly toothed on apical 2/3; apex acute to acuminate; veins with sparse slender white hairs when young; basal lateral veins extending to middle of blade or beyond; secondary veins 4 or 5 on each side of midvein and abaxially prominent; petiole 4-8 cm. **Figs**: clustered on short branchlets of old stems, dark red when mature, pear-shaped to globose, with 4-6 longitudinal ridges and small tubercles, 2-3.5 cm in diam., puberulent, basally attenuated into a short stalk, apical pore depressed, bracts ovate and rosulate; peduncle 2.5-3.5 cm; involucral bracts triangular-ovate. **Male flowers**: near apical pore; shortly pedicellate; perianth 3, connate, thinly membranous; stamens 2; filament long. **Gall flowers**: many, on middle or lower part of fig; pedicellate to sessile; perianth 3, connate, narrow lanceolate, thinly membranous; ovary obovoid; style lateral, short. **Female flowers**: pedicellate; perianth 3, narrow lanceolate; style lateral, longer than in gall flowers. **Fruit**: achenes, obovoid, smooth, 1.5x2 mm.

Flowering: September-April **Fruiting:** May-June

Ecology: valleys, along streams or moist soil areas, 500-2,100 m

Pollinator: *Ceratosolen emarginatus* Mayr

21. ***Ficus semicordata*** **Buch.-Ham. ex Sm.**

เดื่อปล้องหิน (Duea plong hin) (Figure 4.27, 4.40, 4.41)

Trees, 3-10 m tall, crown flat, spreading and umbrella-like; bark gray, smooth; branchlets white or brown pubescent; stipules red, lanceolate, 2-3.5 cm, membranous, subglabrous. **Leaf**: distichous, densely covered with stiff hairs; blade oblong-lanceolate, strongly asymmetric, 18-28 × 9-11 cm; base obliquely cordate on one side and auriculate on other side; margin with small teeth or entire; apex acuminate; basal lateral veins 3 or 4 on auriculate side of leaf blade, and extending into auriculate base; secondary veins 8-14 on each side of midvein; petiole thick, 5-10 mm. **Figs**: on pendulous, eventually prostrate, leafless branchlets, underground at maturity; solitary, reddish purple when mature, globose, 1-1.5 cm in diam., stiffly hairy; peduncle 5-10 mm; involucral bracts pubescent; lateral bracts present. **Male flowers**: near apical pore; perianth 3, red, lanceolate, longer than stamens, stamens 1 or 2; filaments short; anthers white. **Gall flowers**: perianth 4 or 5, linear-lanceolate; style lateral, short. **Female flowers**: basal bracteole 1; perianth 4 or 5; ovary ovoid-ellipsoid; style lateral, long; stigma cylindric, shallowly 2-lobed. **Fruit:** achenes, broadly ovoid, 1x1.5 mm.

Flowering: March, August, December **Fruiting:** April, September, January

Ecology: forest margins, valleys, along trails, 600-1,900 m

Pollinator: *Ceratosolen gravelyi* (Grandi)

22. *Ficus squamosa* Roxb.

เดื่อผา (Deua pha) (Figure 4.28, 4.38)

Shrubs, small, erect, rooting adventitiously; branchlets and petioles densely coarsely brown hairy. Stipules lanceolate, 5-10 mm. **Leaf**: spirally arranged, clustered apically on branchlets, densely covered with stiff thick rust-colored hairs; blade oblanceolate to oblong, 4.5-13 × 1.2-3.2 cm, papery, with long thick rust-colored hairs on midvein but sparsely pubescent on other veins; base narrowly cuneate; margin entire or apically sparsely toothed; apex acuminate; basal lateral veins short; secondary veins 6-8 on each side of midvein, apically curved and looped at margin.; petiole 0.5-1 cm. **Figs**: axillary or branchlets from old stems, solitary, globose, 1.5-2 cm in diam., with prominent longitudinal ridges, densely covered with thick rust-colored hairs or villous, basally attenuated into a ca. 8 mm stalk; pedunculate; involucral bracts unequal. **Male flowers**: perianth 3 or 4; stamen 1; anther ovoid to obovoid. **Gall flowers**: subsessile; perianth absent; ovary smooth; style lateral, short, stigma tubular. **Female flowers**: similar to gall flowers; style persistent silk-like, with long hairs. **Fruit**: achenes rhombic-ovoid, with hairs, 1x1 mm

Flowering: January-March, May-July **Fruiting:** April-May, July-October

Ecology: moist forests, near the stream or on the rock in stream and falls, 700-1,200 m

Pollinator: *Ceratosolen* sp.

23. ***Ficus variegata*** **Blume**

ผูก (Phuk) (Figure 4.29)

Trees, 7-15 m tall; bark gray to grayish brown, smooth; branchlets green, sparsely pubescent. Stipules ovate-lanceolate, 1-1.5 cm, glabrous. **Leaf**: alternate; leaf blade broadly ovate to ovate-elliptic, 10-17 cm, thick papery, pubescent when young; base rounded to shallowly cordate; margin entire, undulate, or shallowly toothed; apex acute, acuminate, or obtuse; basal lateral veins 4, outer 2 thin and short; secondary veins 4-16 on each side of midvein; petiole 2.5-6.8 cm. **Figs**: clustered on shortly tuberculate branchlets from old stem, red, with green stripes and spots when mature, globose to depressed globose, 2.5-3.5 cm in diam., apex slightly depressed and navel-like; apical pore convex; bracts ovate; peduncle 2-4 cm, slender; involucral bracts caduceus; scar ringlike. **Male flowers**: near apical pore, sessile; perianth 3 or 4, broadly ovate; stamens 2, filaments basally connate. **Gall flowers**: near apical pore; calyx 4- or 5-lobed; transparent, membranous, lanceolate; style lateral, short; stigma funnelform. **Female flowers**: perianth 3 or 4, connate at base, thinly membranous, linear lanceolate; style persistent, as long as achenes, broadly in the mid; stigma clavate, glabrous. **Fruit:** achenes obovoid, finely tuberculate, 1.5x1 mm.

Flowering: April-May, December-January **Fruiting:** May, January

Ecology: valleys or moist open areas

Pollinator: *Ceratosolen appendiculatus* Mayr

Subgenus *Ficus*

24. ***Ficus ischnopoda*** **Miq.**

ลูกคล้าย (Luk khlai) (Figure 4.30, 4.39, 4.41)

Shruby trees, 2-3 m tall; bark gray; branchlet internodes red, short. Stipules linear-lanceolate, ca. 8 mm. **Leaf**: clustered apically on branchlets; blade elliptic-lanceolate to oblanceolate, 4-13 × 1.3 cm, both surfaces glabrous; apex acuminate; basal lateral veins short; secondary veins 7-15 on each side of midvein, and apically curved; petiole 5-8 mm. **Figs**: axillary on leafy or older leafless branches, solitary or occasionally paired, conic to spindle-shaped, with longitudinal ridges 1.2 × 0.5-0.8 cm; basally attenuate into a short stalk; peduncle 1-1.5 cm; involucral bracts 3 or 4, semipersistent. **Male flowers**: near apical pore; pedicellate; perianth 3 or 4, oblanceolate; stamens 2; anthers ellipsoid. **Gall flowers**: subsessile; perianth 4, short; ovary globose; style lateral, short. **Female flowers**: subsessile; perianth 4, short; style persistent, long; stigma 2-lobed, hairs. **Fruit:** achenes, reniform, 1x1.5 mm

Flowering February-June **Fruiting:** May-August

Ecology: river banks, on the crack rock in the stream or falls, 310-2,200 m

Pollinator: *Blastophaga* sp.

25. *Ficus hirta* Vahl

เดื่อขน (Duea Khon) (Figure 4.31)

Shrubs or small trees; branchlets leafless in middle, golden yellow or brown hirsute. Stipules red, ovate-lanceolate, 1.3 cm, membranous, pubescent. **Leaf**: alternate, brown hirsute; blade simple or palmately 3-5-lobed, 8x25 cm, glabrous or golden yellow hirsute; base cuneate; rounded, or shallowly cordate; margin entire or with small serrations; apex acute to acuminate; basal lateral veins 2-4; secondary veins 4-7 on each side of midvein; petiole 1.8 cm. **Figs**: axillary on normal leafy shoots, paired, globose, 1-3 cm in diam., with long stiff spreading golden yellow or brown hairs and also pubescent. **Male flowers**: pedicellate; perianth 4, red, lanceolate; stamens 2 or 3; anthers ellipsoid, longer than filaments. **Gall flowers**: sessile; perianth 4, broadly lanceolate; ovary globose, smooth; style lateral, short; stigma funnelform. **Female flowers**: sessile or pedicellate; perianth 4; style persistent, long, thin; stigma clavate. **Fruit:** achenes ellipsoid-globose, smooth, 1x1.5 mm.

Flowering: December, April, September **Fruiting:** January, May, October

Ecology: forests, forest margins, open areas; low elevations

Pollinator: *Blastophaga javana* Mayr

Subgenus *Synoecia*

26. ***Ficus anserina*** **Corner** - (Figure 4.32, 4.39, 4.41)

Shrubs, scandent; old branchlets glabrous, young branchlets densely covered with coarse dark brown hairs. Stipules caducous, lanceolate, ca. 4 cm. **Leaf**: distichous, sparsely pubescent; blade brown when dry, oblong to narrow elliptic, 30-35 × 10-15 cm, leathery, densely covered with brownish red short pubescence; base cuneate to occasionally rounded; margin entire; apex shortly acuminate; basal lateral veins not extending to 1/3 of leaf blade length; secondary veins 5-7 on each side of midvein, petiole ca. 1 cm. **Figs**: pear-shaped, 6-9 × 4-6 cm, ridged on surface, densely covered with rust-colored scale-like hairs; peduncle 3-15 mm. **Male flowers**: near apical pore; pedicel long; perianth 4, oblanceolate, unequal in size; stamens 2; filaments very short; anthers oblong, mucronate. **Gall flowers**: perianth 5, slightly recurved; involucral bracts reniform, pubescent, spatulate; style subapical. **Female flowers**: subsessile; perianth 4; style subapical, long. **Fruit**: achenes oblong, slightly depressed, 2-2.5 mm.

Flowering: March-May, Septeber **Fruiting:** June-August, October

Ecology: rain forests, forests, mountain slopes, limestone areas, 400-1400 m

Pollinator: not seen in study areas

27. ***Ficus pumila*** **L.**

มะเดื่อเถา (Ma duea thao) (Figure 4.33, 4.39, 4.41)

Shrubs, climbers or scandent; rooting branchlets sterile. Stipules lanceolate, with yellow brown silk-like hairs. **Leaf**: distichous; blade different in shape, ovate-cordate, ovate-elliptic, or oblong-ovate, 5-12 × 2-5 cm; base rounded to slightly cordate; margin entire; apex obtuse, acute, or acuminate; veins conspicuous, honey comb-like; basal lateral veins elongated; secondary veins 3 or 4 on each side of midvein. **Figs**: axillary on normal leafy branches, solitary, yellowish green to pale red when mature, pear-shaped to globose or cylindric, 4-8 × 3-5 cm, shortly yellow pubescent when young; basally attenuate into a short stalk; apical pore truncate, or acuminate; peduncle to ca. 1 cm, thick; involucral bracts triangular-ovate, densely covered with long pubescence, persistent. **Male flowers**: many, in several rows near apical pore; pedicel long, perianth 3 or 4, linear; stamens 2; filaments short. **Gall flowers**: sessile; perianth 3 or 4, linear; style lateral, short; stigma funnelform. **Female flowers**: pedicellate; perianth 4. **Fruit**: achenes, globose, 2x2.5 mm.

Flowering: May-August **Fruiting:** May-August

Ecology: cultivated plant, native plant from South China through Malaysia

Pollinator: not seen in study areas

Subgenus ***Sycidium***

28. ***Ficus anastomosans*** **Berg** - (Figure 4.34, 4.40)

Shrubs, terrestrial, sometime subscandent. growing on the rock; bark slightly coarse. Branchlets drying brown. **Leaf**: distichous; lamina elliptic to ovate-elliptic, asymmetric, 3.5-7 × 2.5-4 cm, subcoriaceous; base round to obtuse; margin crenate-dentate to sublobate; apex obtuse to acute; basal lateral veins short; secondary veins 5-7, on each side of midvein; petiole thick, 3-5 mm. **Figs**: axillary on normal leafy shoots, solitary or paired, globose or subglobose-shaped, 4-7 mm in diam., hairy; peduncle very short, purple red in seed fig and orange yellow in gall fig. **Male flowers**: sessile; perianth 2-3, lanceolate; stamen 2; filament long, red. **Gall flowers**: pedicellate; perianth 3-4, transparent; style short, lateral; ovary obliquely ovoid. **Female flowers**: perianth 3-4, thin, transparent, linear; style persistent, lateral, short; stigma enlarged. **Fruit**: achenes ellipsoid, keeled, with tubercles, 1x1 mm.

Flowering: May-July **Fruiting:** July-August

Ecology: limestone mountain, crack of the rock, open and dry areas, 500-900 m

Pollinator: *Liporrhopalum* sp. (Figure 4.42)

29. ***Ficus subincisa*** **Buch.-Ham. ex Smith**

มะเดื่อน้อย (Ma duea noi) (Figure 4.35, 4.40)

Shrubs or small trees, 1-3 m tall; bark dark grayish; branchlets reddish brown, slender, narrowly winged. Stipules caducous, linear to lanceolate, ca. 5 cm. **Leaf**: blade obovate-oblong to elliptic-lanceolate, 4-12 × 2-5 cm, papery; base cuneate; margin apically undulate or with a few blunt teeth; apex long-caudate; basal lateral veins short; secondary veins 5-7 on each side of midvein; oblique to near margin then looped; petiole 4-6 mm. **Figs**: axillary on normal leafy shoots, solitary, when mature, reddish orange in seed fig and yellow in gall fig, ellipsoid to globose, 0.6-2.5 cm in diam., smooth or tuberculate and lenticellate; peduncle 2-10 mm; involucral bracts triangular. **Male flowers**: near apical pore; pedicellate; perianth 4; stamen 1. **Gall flowers**: subsessile; perianth 3; ovary smooth; style lateral; stigma shortly funnelform. **Female flowers**: pedicellate; perianth 3; style lateral, long; stigma enlarge. **Fruit**: achenes, lens-like, smooth, 1x1 mm.

Flowering: May-July **Fruiting:** September-October

Ecology: moist forests, along streams, valleys, 400-2,000 m

Pollinator: *Liporrhopalum* sp.

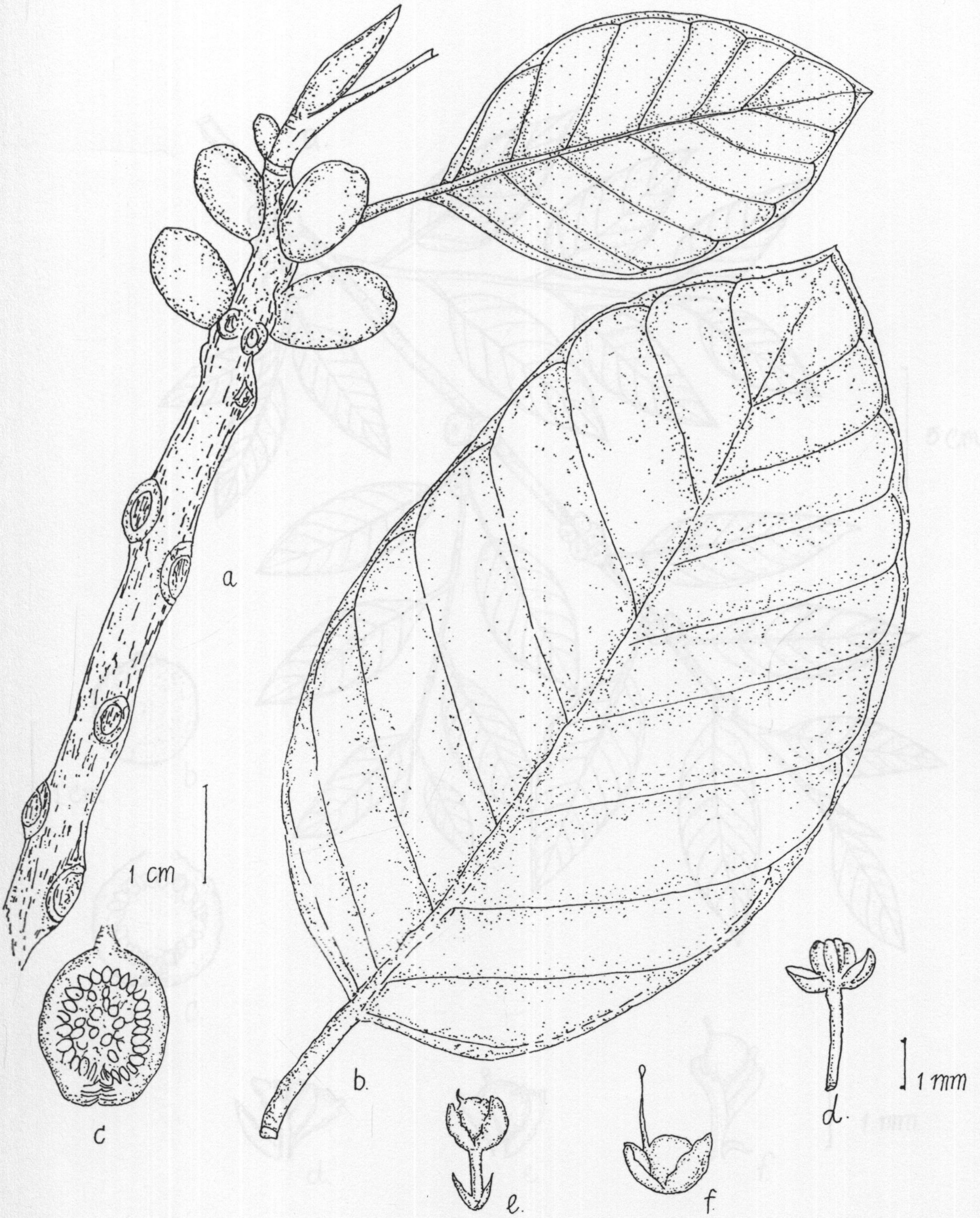


Figure 4.9 *Ficus altissima* Bl.; a. fruiting branch, b. leaf, c. long section of syconium, d. male flower, e. gall flower, f. female flower (seed)

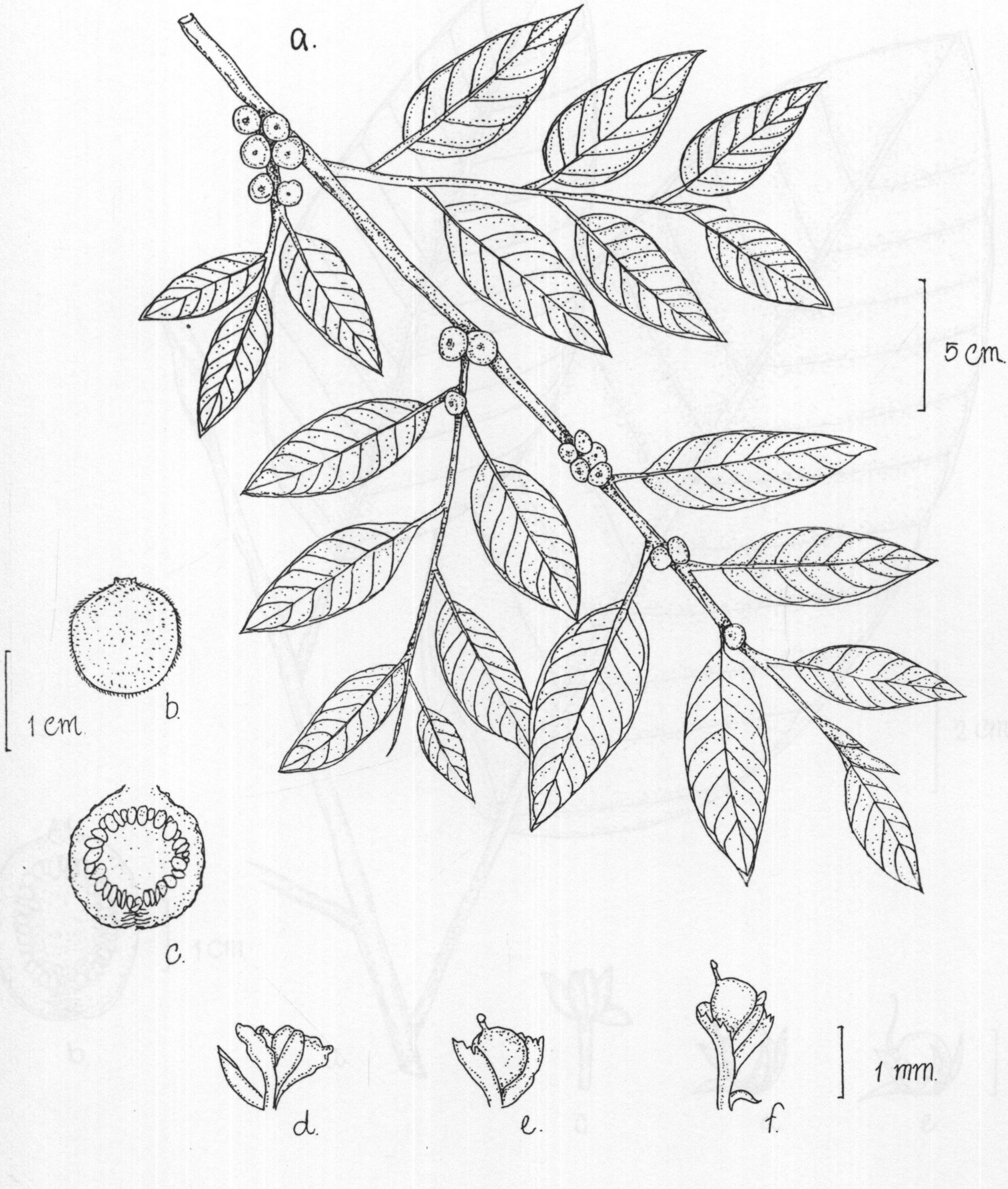


Figure 4.10 *Ficus benjamina* L.; a. fruiting branch and leaves, b. hairy fruit of *F. benjamina var. nuda* (Miq.) Barrett., c. long section of syconium, d. male flower, e. gall flower, f. female flower (seed)

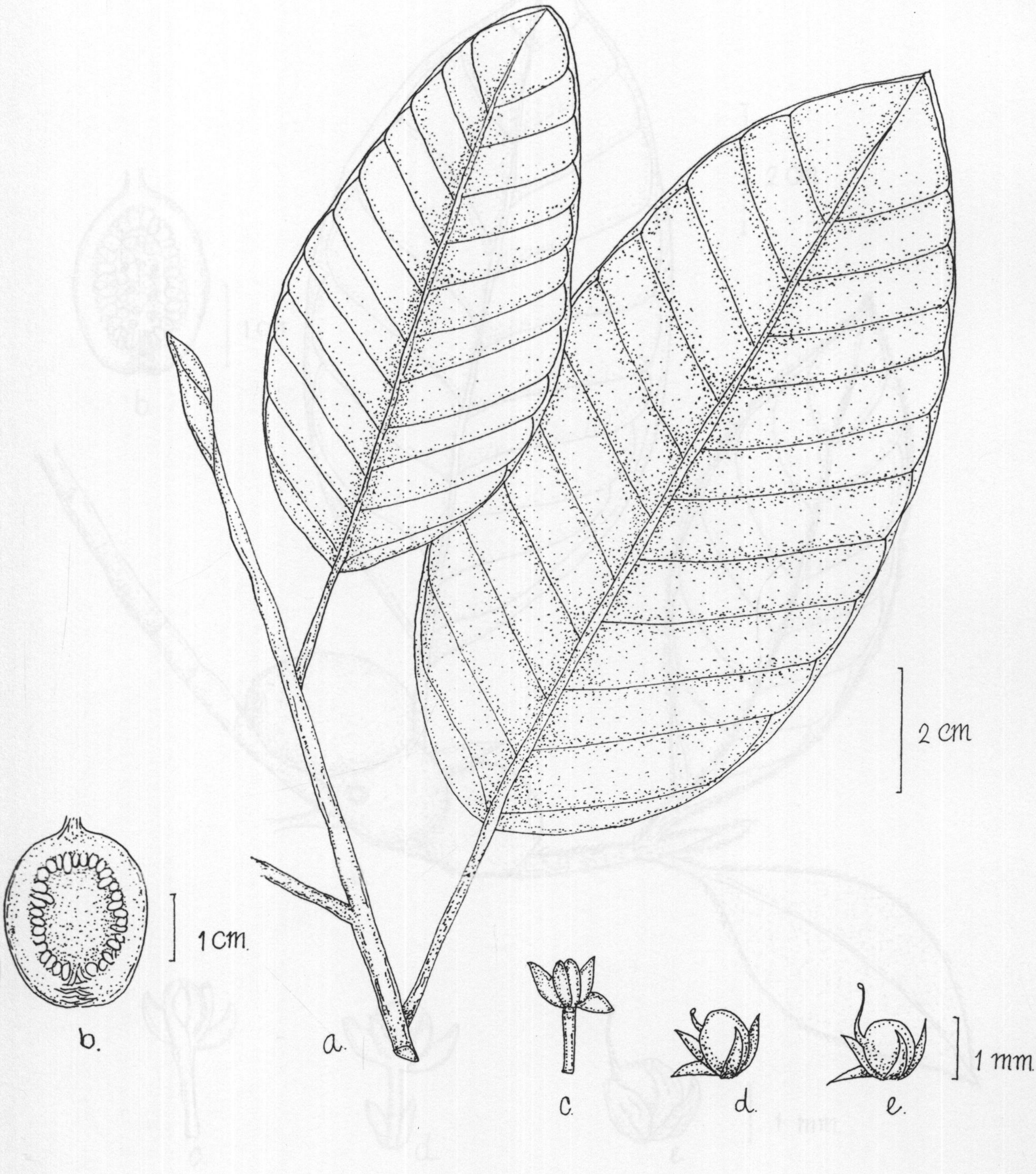


Figure 4.11 *Ficus curtipes* Corner; a. leaves, b. long section of syconium c. male flower, d. gall flower, e. female flower (seed)

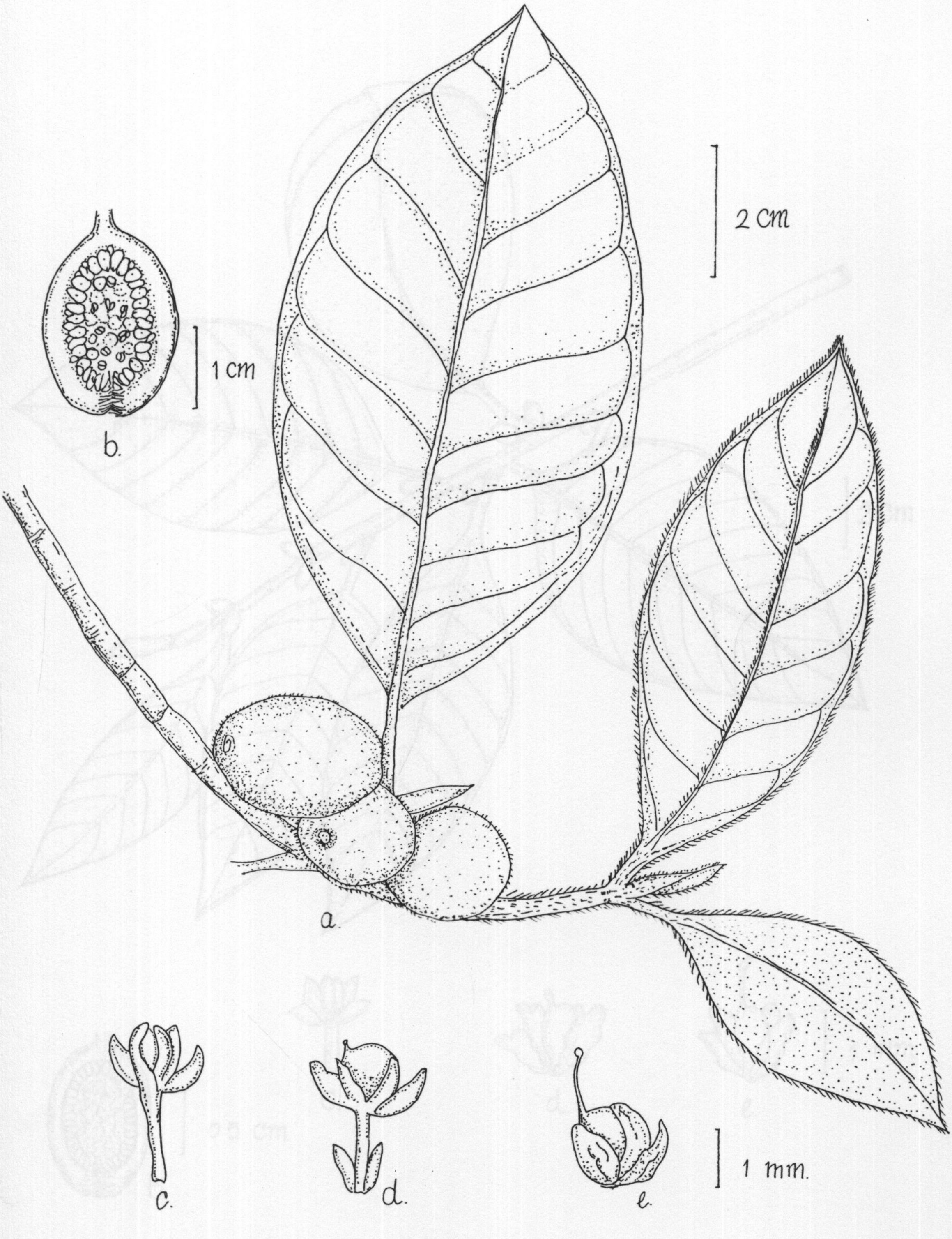


Figure 4.12 *Ficus drupacea* Thunb.; a. fruiting branch, b. long section of syconium c. male flower, d. gall flower, e. female flower (seed)

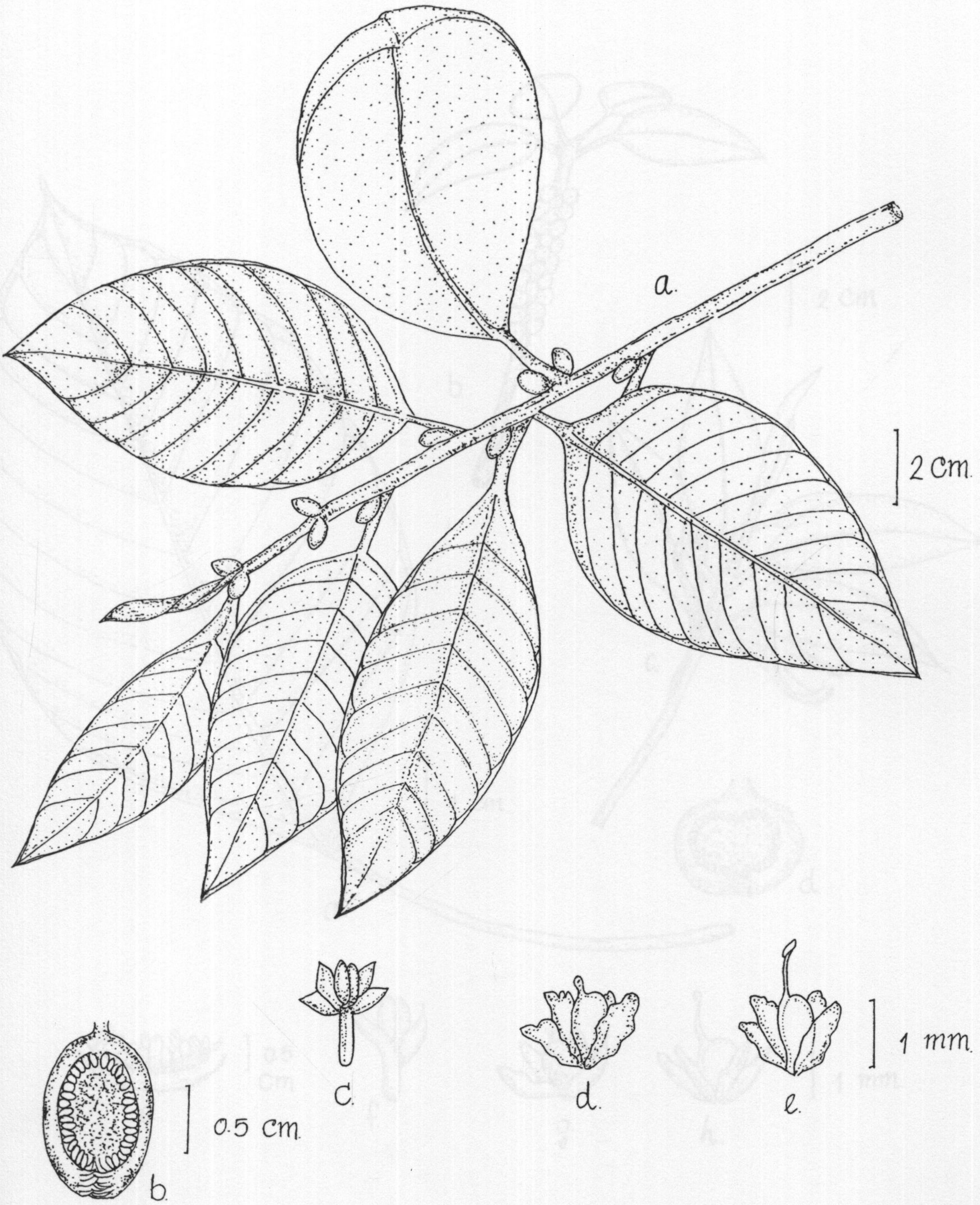


Figure 4.13 *Ficus elastica* Roxb.; a. fruiting branch, b. long section of syconium c. male flower, d. gall flower, e. female flower (seed)

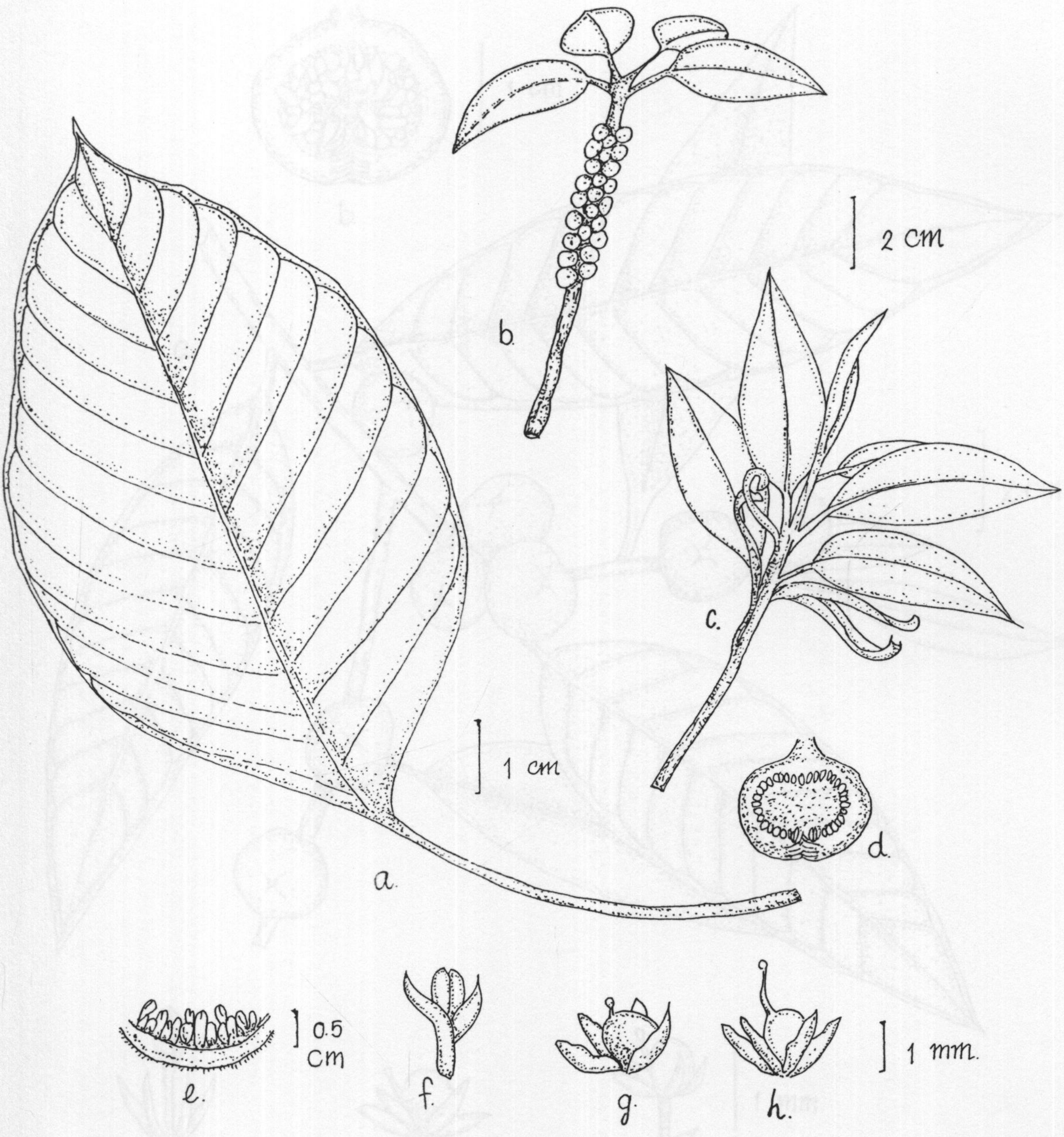


Figure 4.14 *Ficus lacor* Buch. Ham.; a. leaf, b. fruiting branch, c. young leaves and stipule, d. long section of syconium, e. flowers arrangement, f. male flower, g. gall flower, h. female flower (seed)

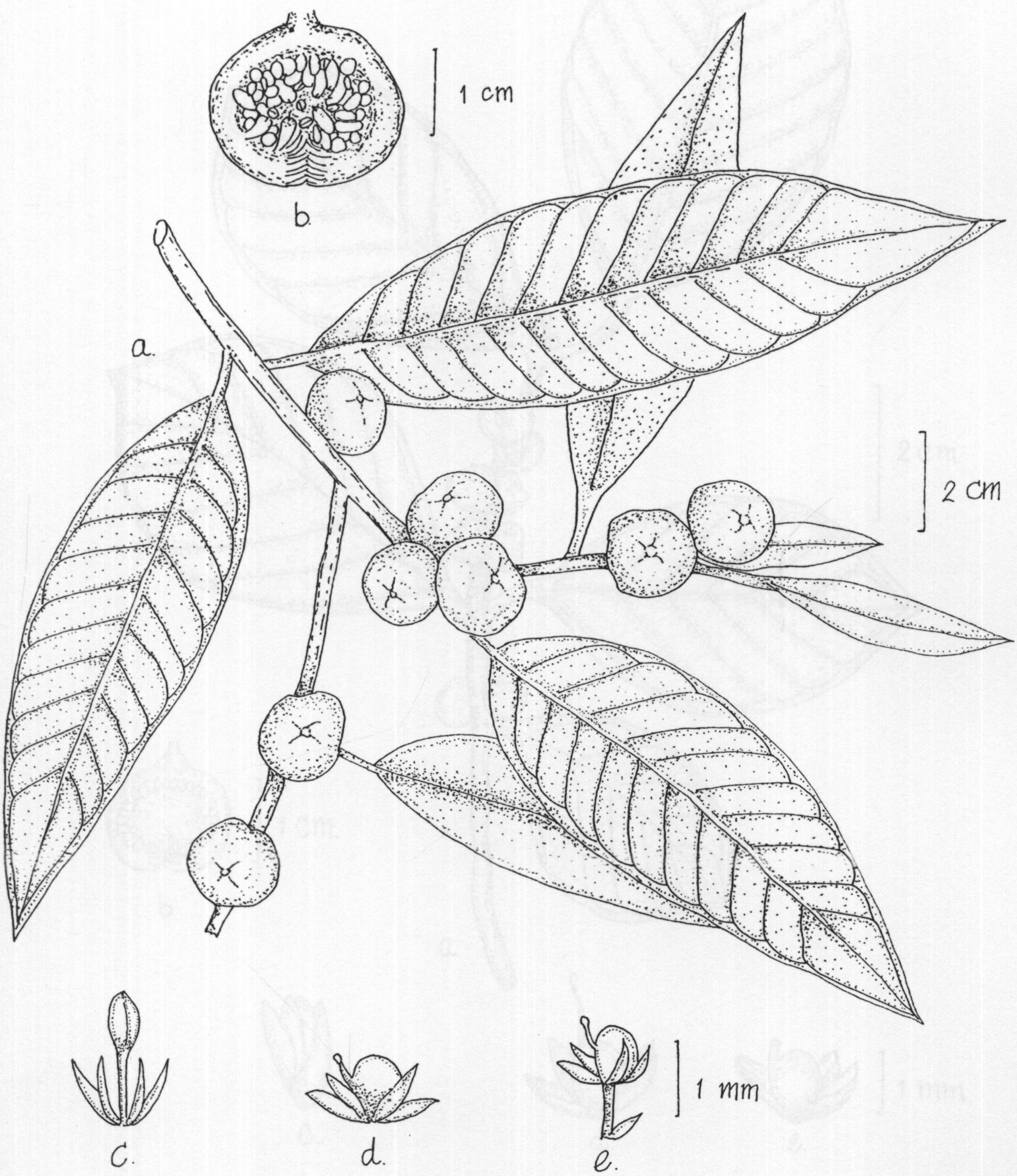


Figure 4.15 *Ficus maclellandii* King; a. fruiting branch, b. long section of syconium, c. male flower, d. gall flower, e. female flower (seed)

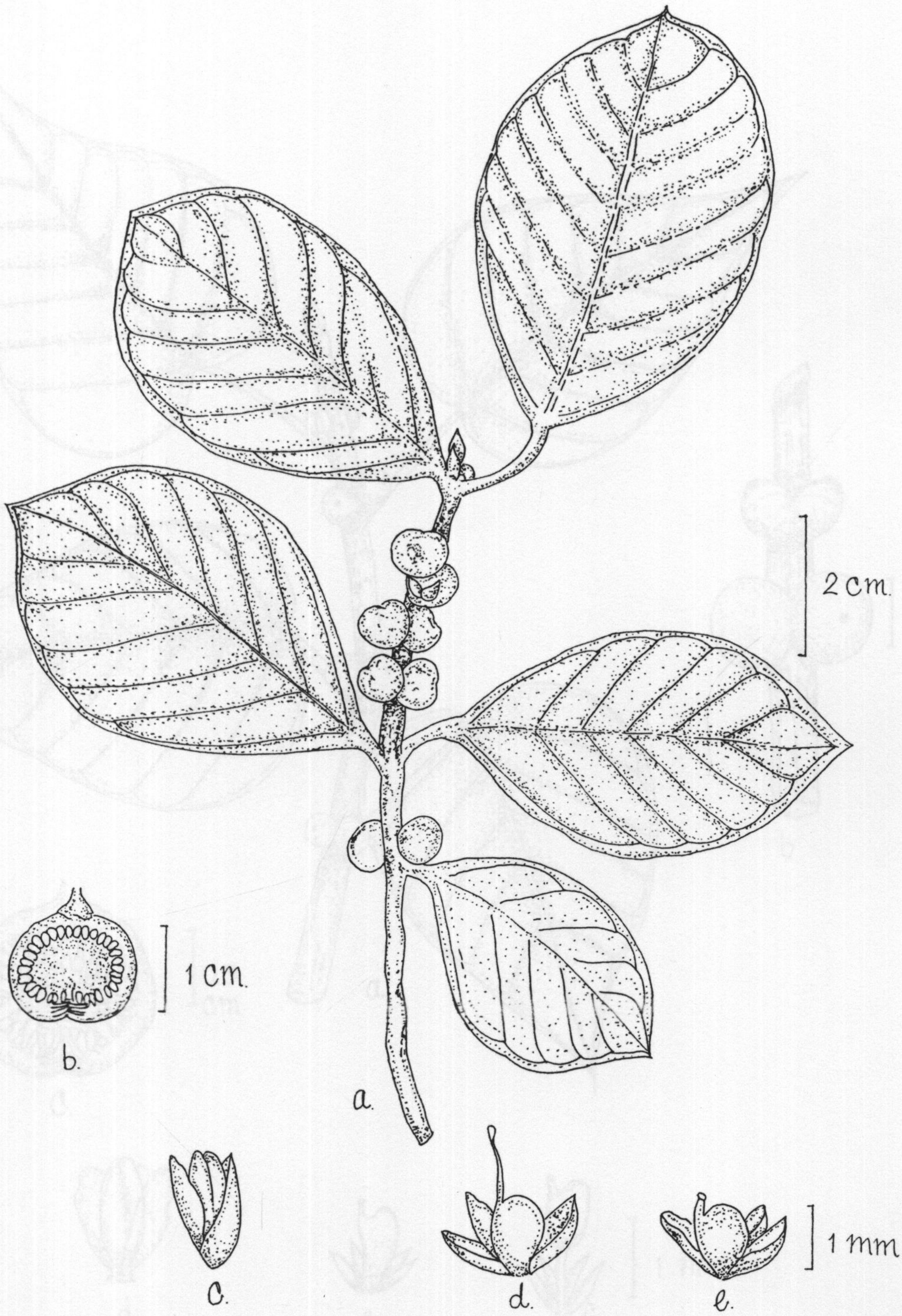


Figure 4.16 *Ficus microcarpa* L. f.; a. fruiting branch, b. long section of syconium, c. male flower, d. female flower (seed), e. gall flower

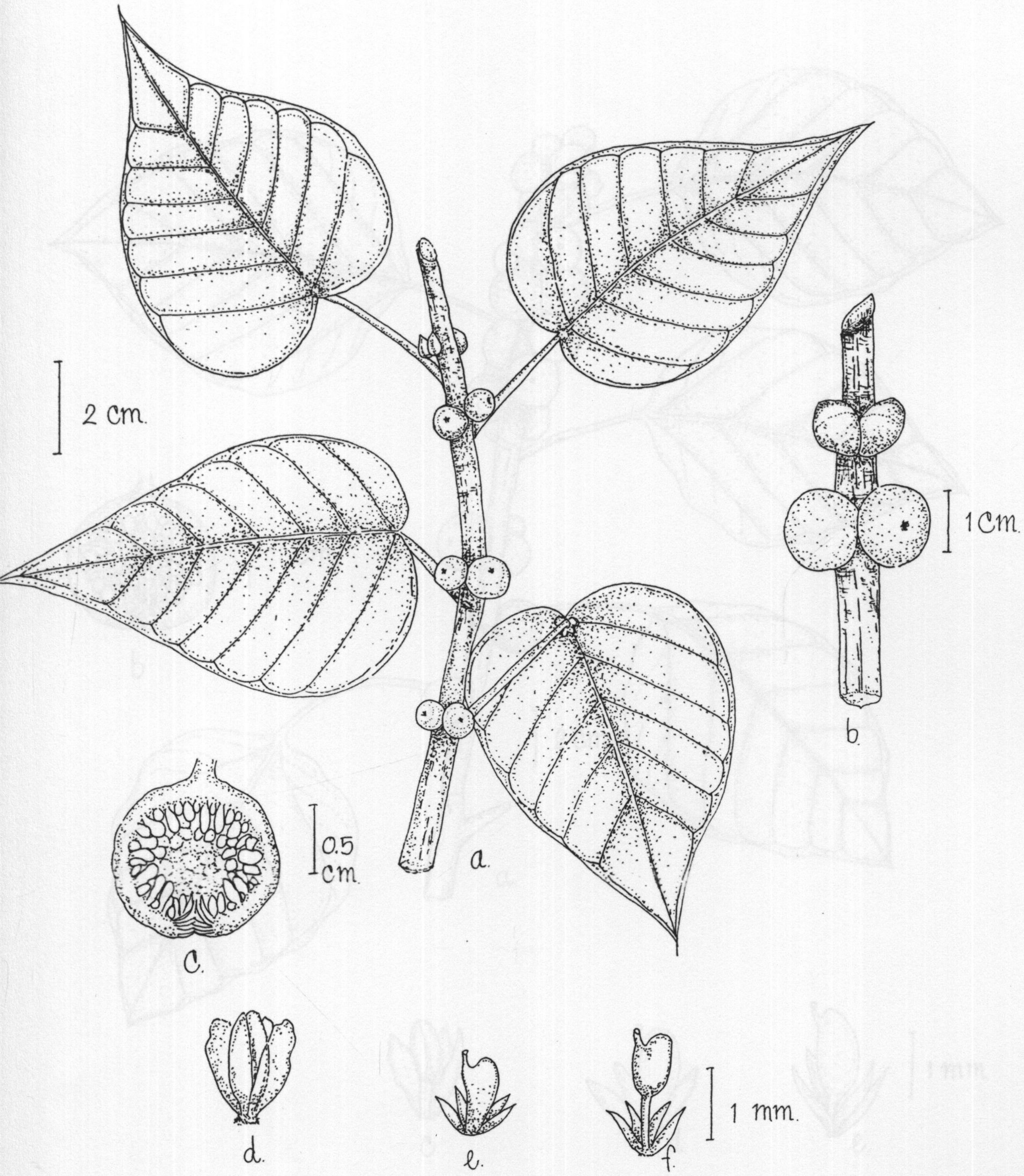


Figure 4.17 *Ficus religiosa* L.; a. fruiting branch, b. pair of fruits, c. long section of syconium, d. male flower, e. gall flower, f. female flower (seed)

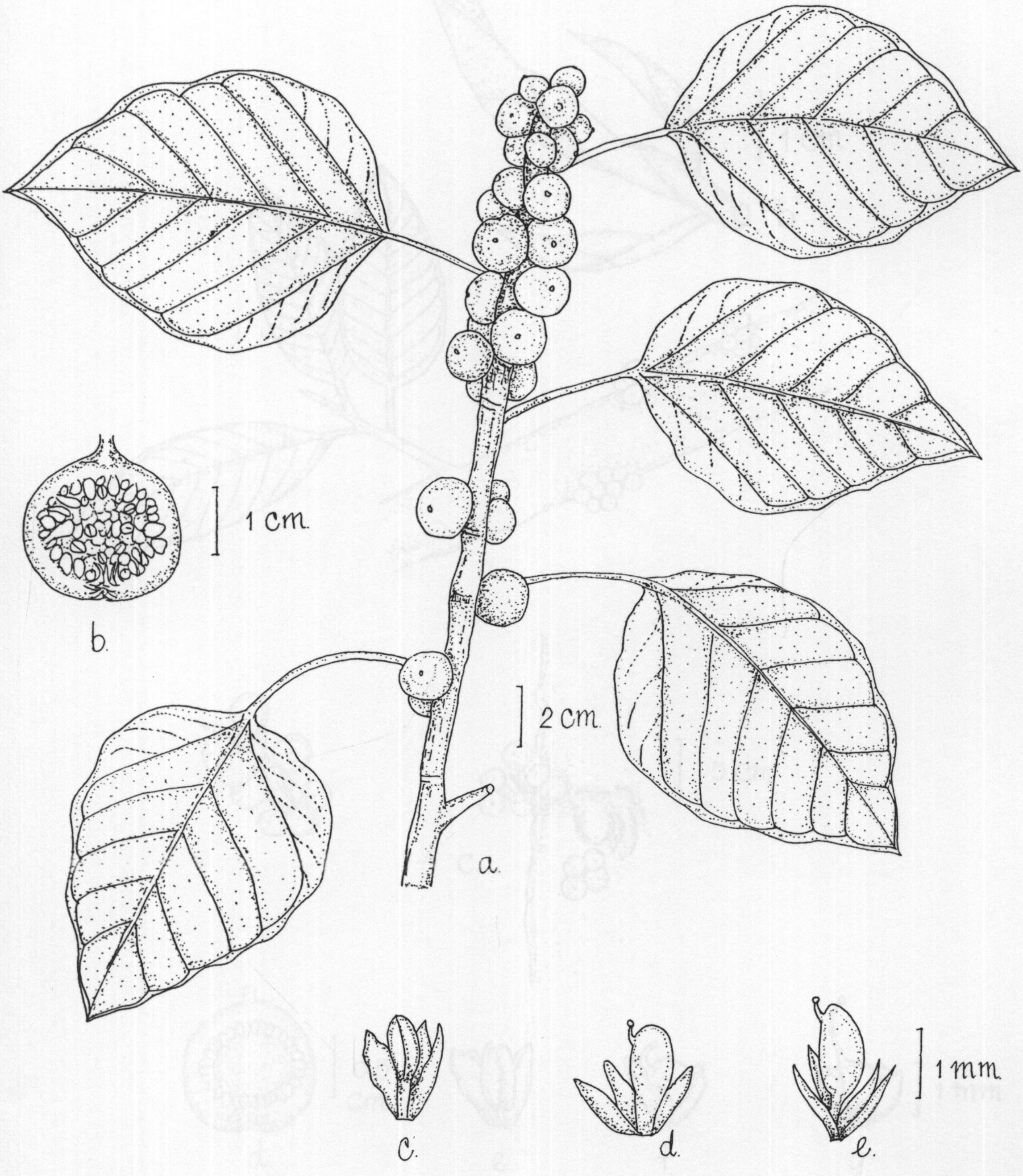


Figure 4.18 *Ficus rumphii* Bl.; a. fruiting branch, b. long section of syconium, c. male flower, d. gall flower, e. female flower (seed)

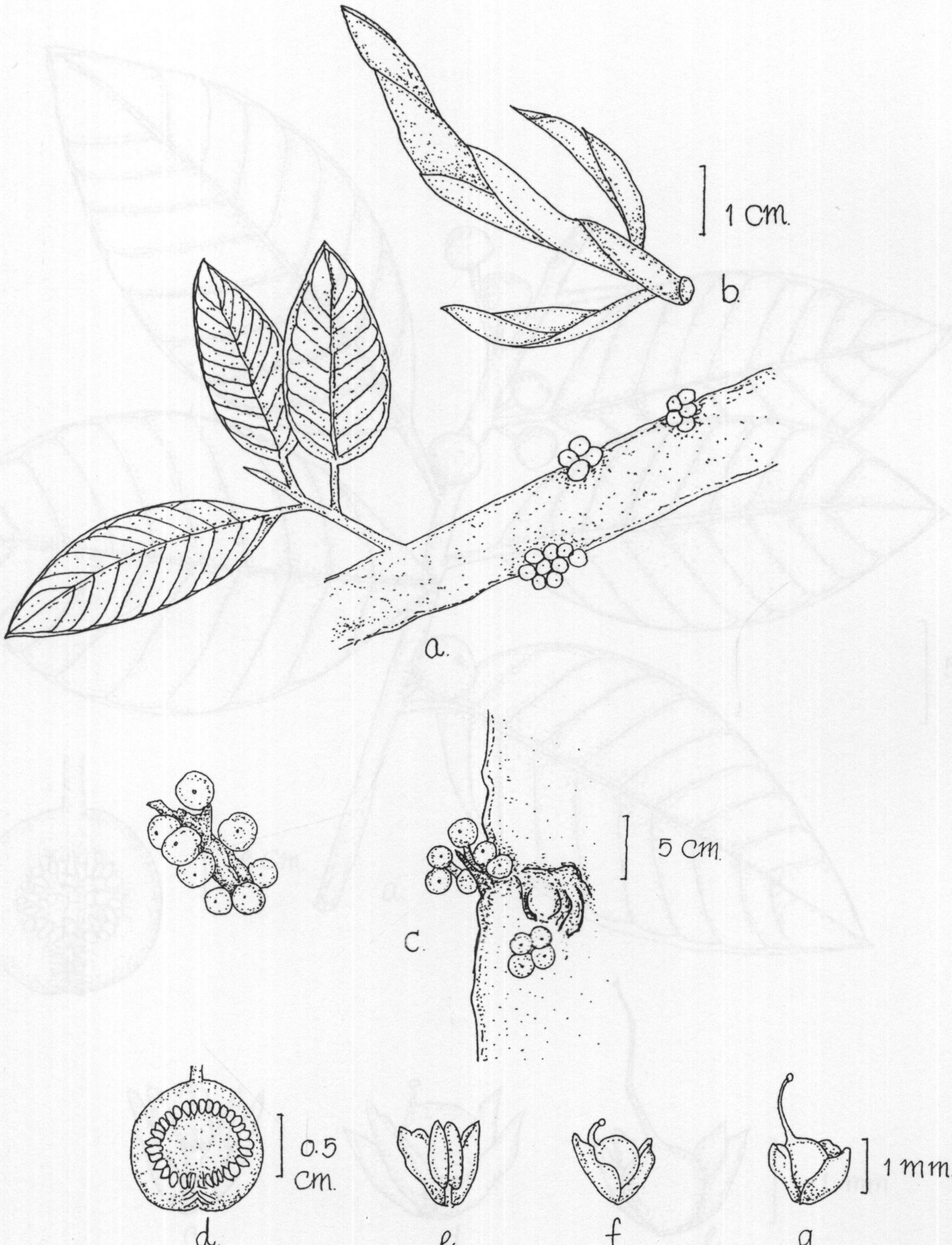


Figure 4.19 *Ficus superba* var. *japonica* Miq.; a. fruiting branch, b. stipule, c. fruiting on trunk, d. long section of syconium, e. male flower, f. gall flower, g. female flower (seed)

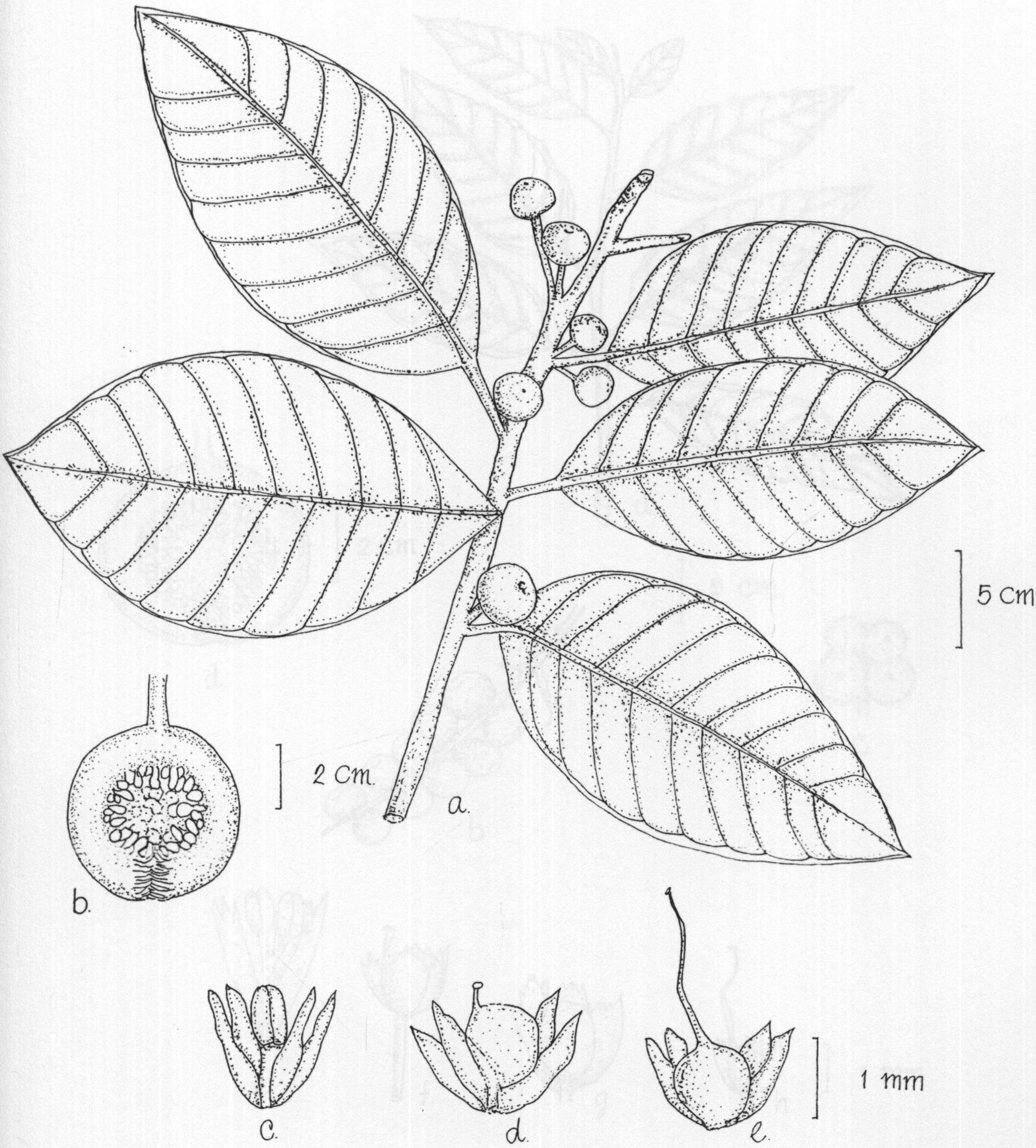


Figure 4.20 *Ficus callosa* Willd.; a. fruiting branch, b. long section of syconium, c. male flower, d. gall flower, e. female flower (seed)

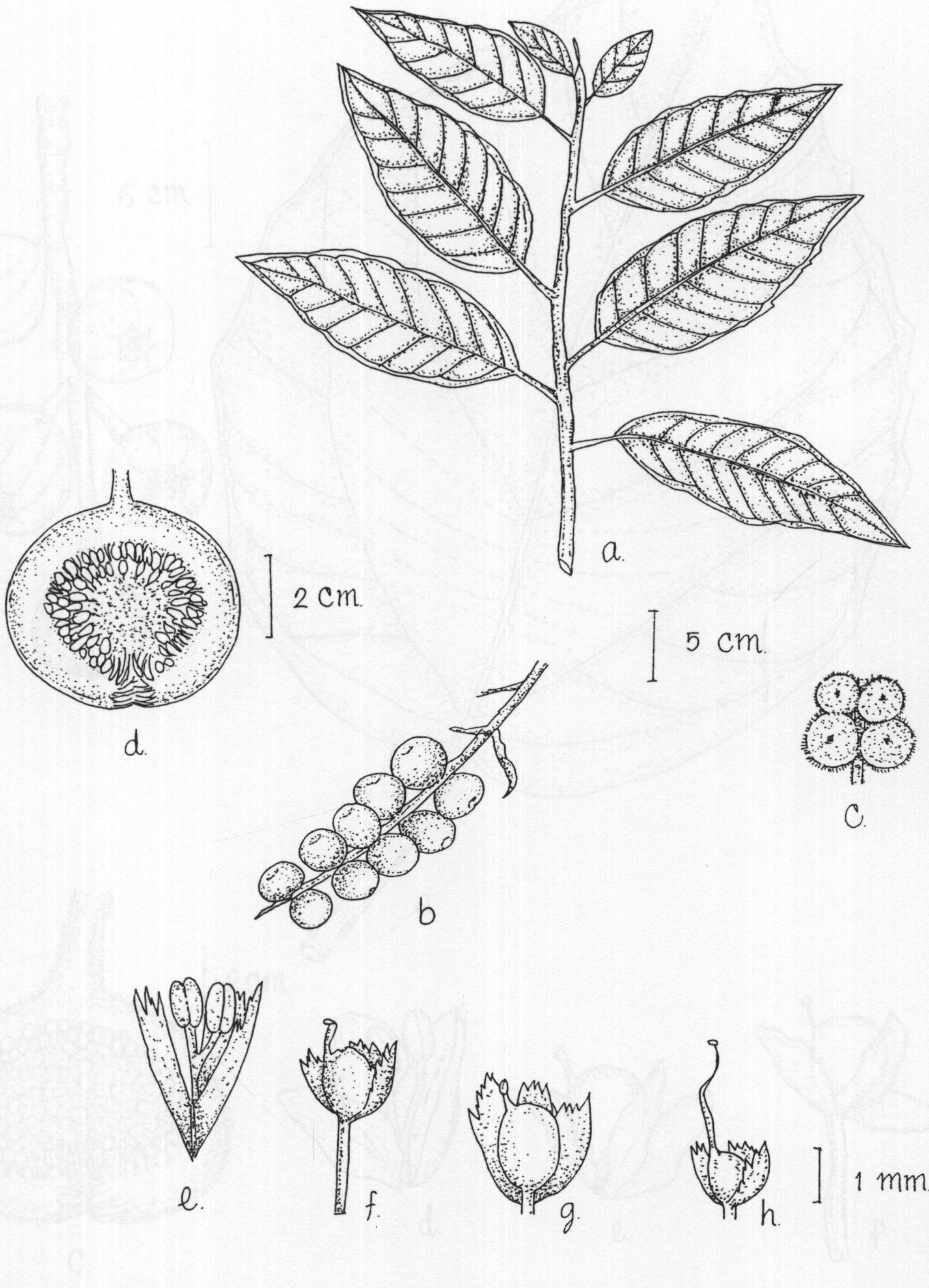


Figure 4.21 *Ficus racemosa* L.; a. leaves, b. fruiting branch, c. hairy fig of *F. racemosa var. miquelli* (King) Corner, d. long section of syconium, e. male flower, f, g. gall flower, h. female flower (seed)

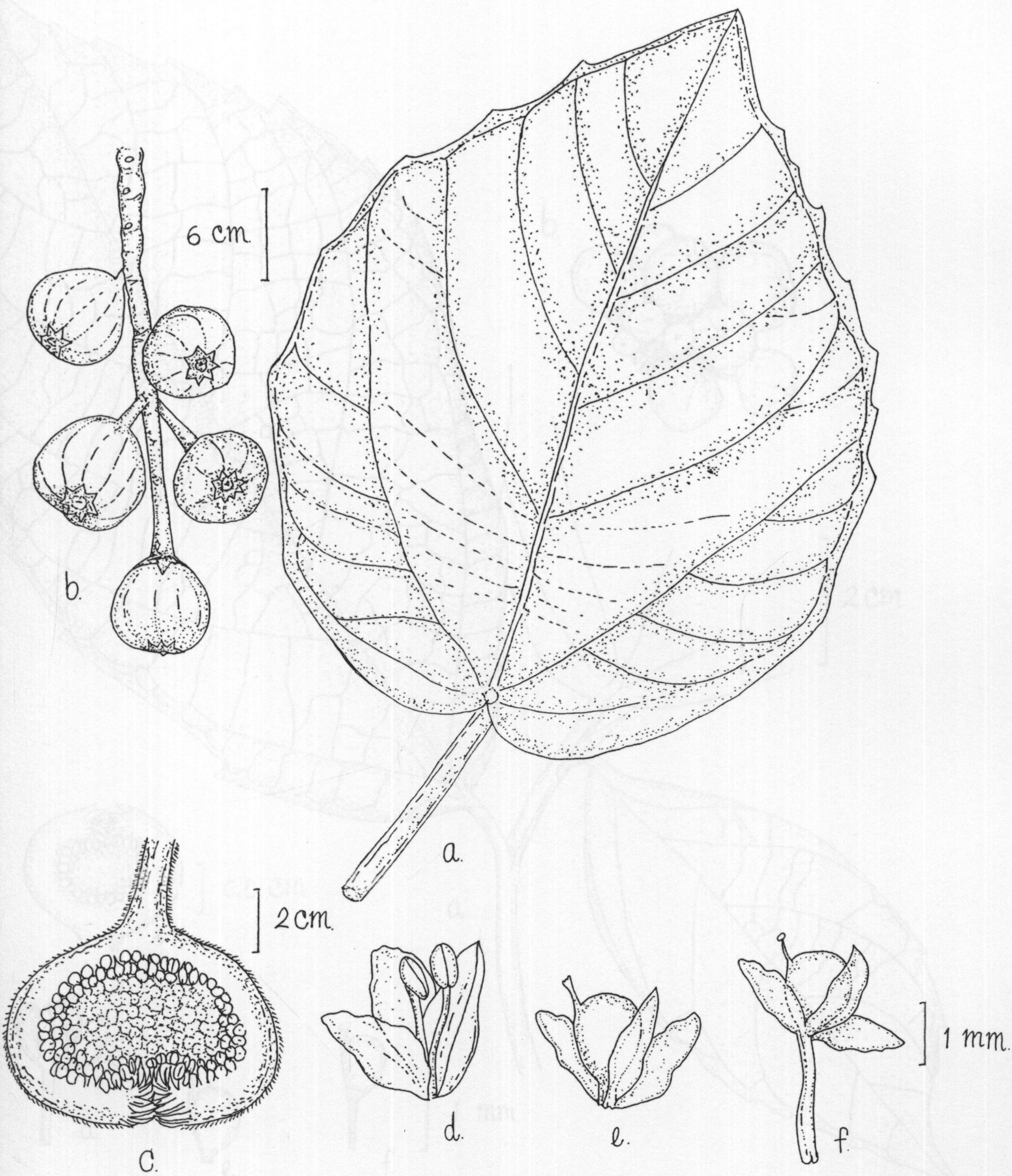


Figure 4.22 *Ficus auriculata* Lour.; a. leaf, b. figs, c. long section of syconium, d. male flower, e. gall flower, f. female flower (seed)

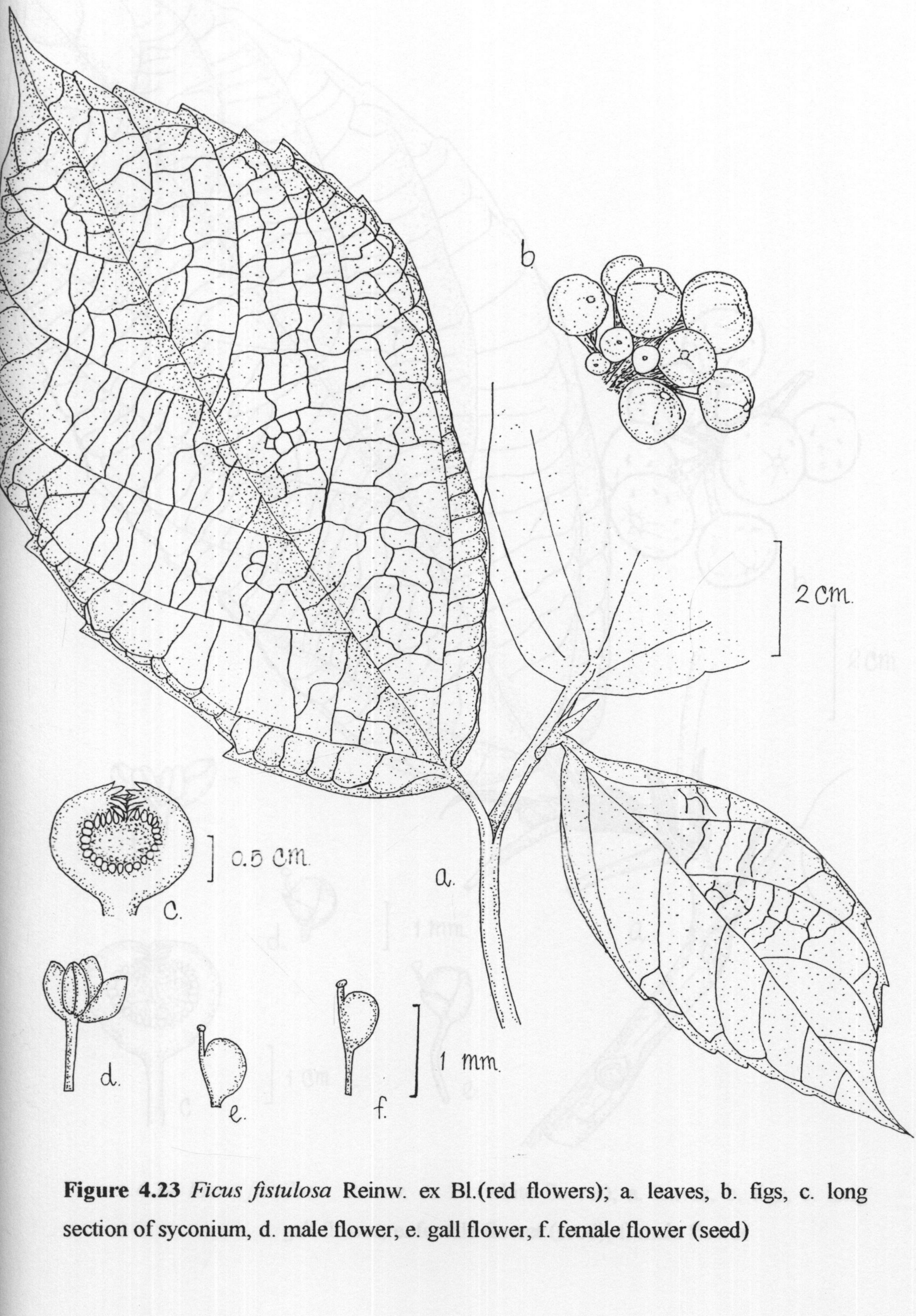


Figure 4.23 *Ficus fistulosa* Reinw. ex Bl.(red flowers); a. leaves, b. figs, c. long section of syconium, d. male flower, e. gall flower, f. female flower (seed)

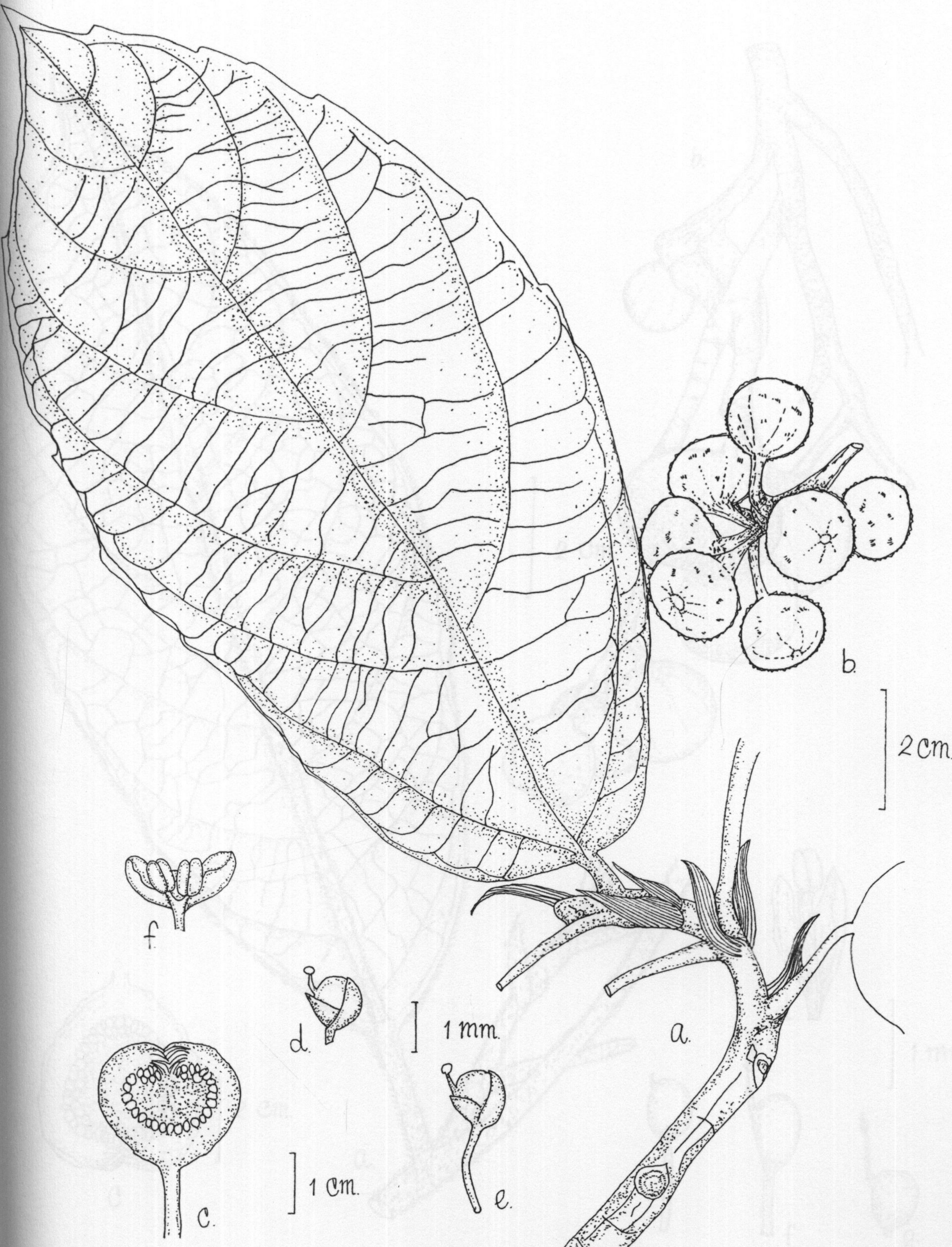


Figure 4.24 *Ficus fistulosa* Reinw. ex Bl.(white flower); a. leaves, b. figs, c. long section of syconium, d. gall flower, e. female flower (seed), f. male flower

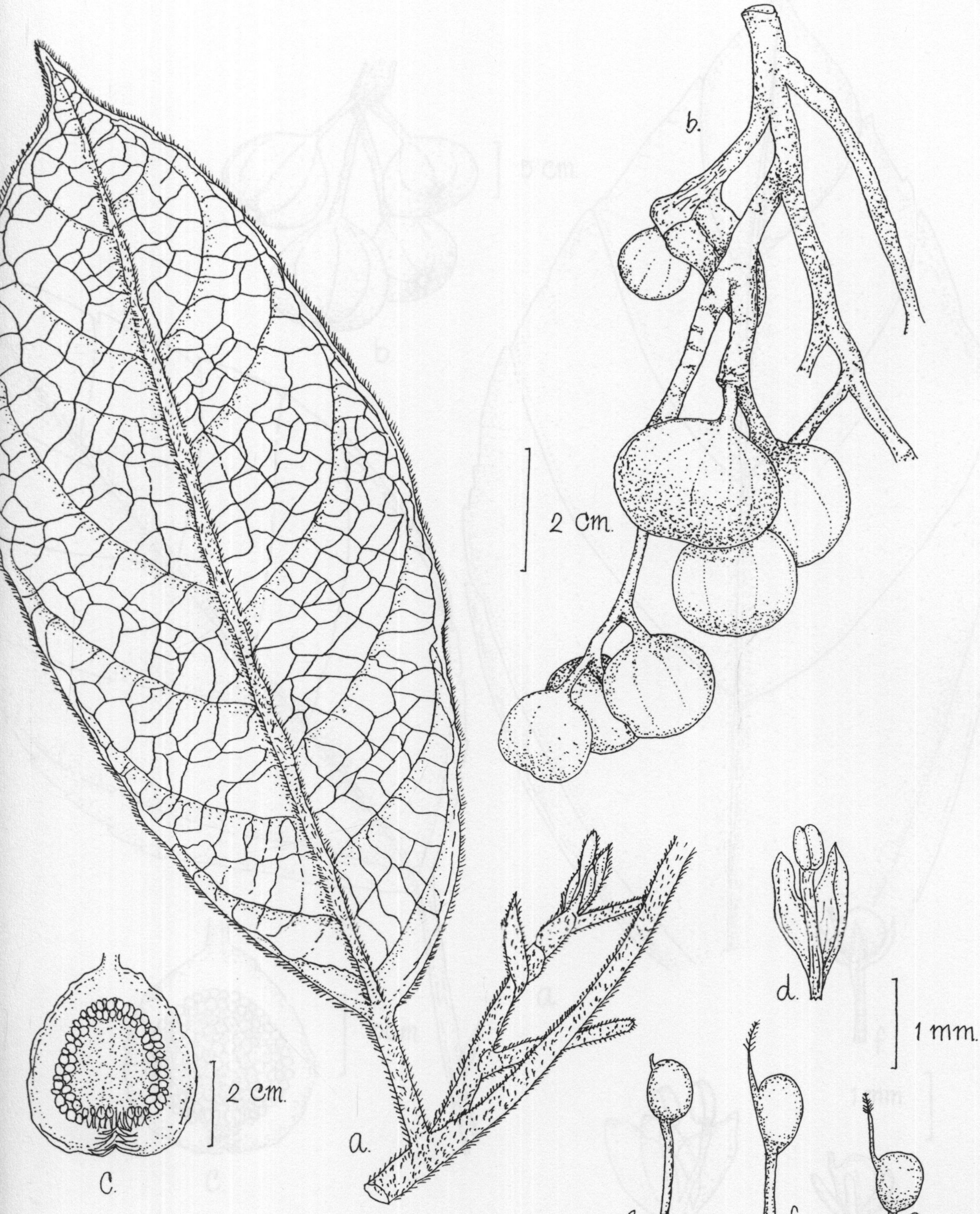


Figure 4.25 *Ficus hispida* L.f. var. *hispida*; a. leaves, b. figs, c. long section of syconium, d. male flower, e. gall flower, f, g. female flower (seed)

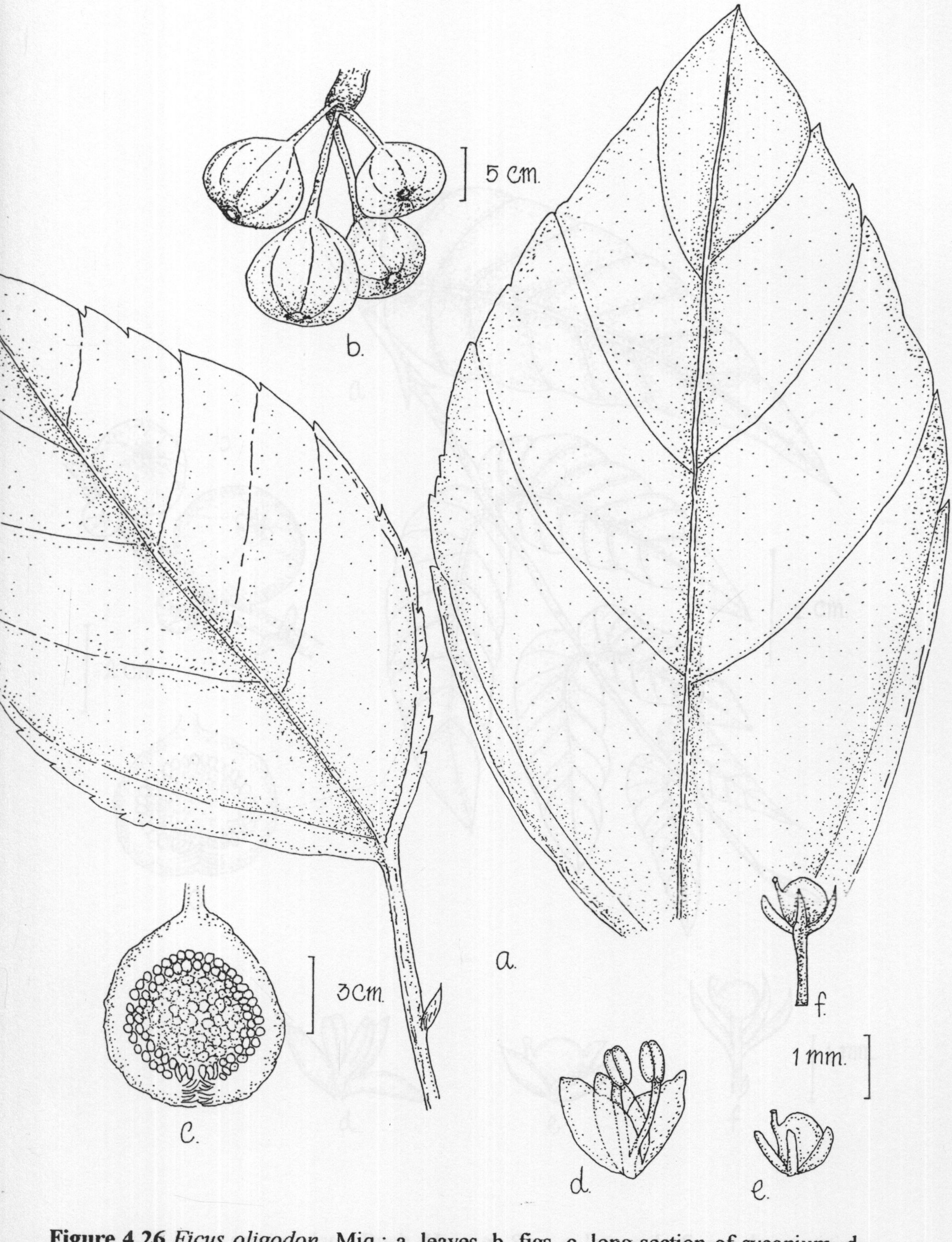


Figure 4.26 *Ficus oligodon* Miq.; a. leaves, b. figs, c. long section of syconium, d. male flower, e. gall flower, f. female flower (seed)

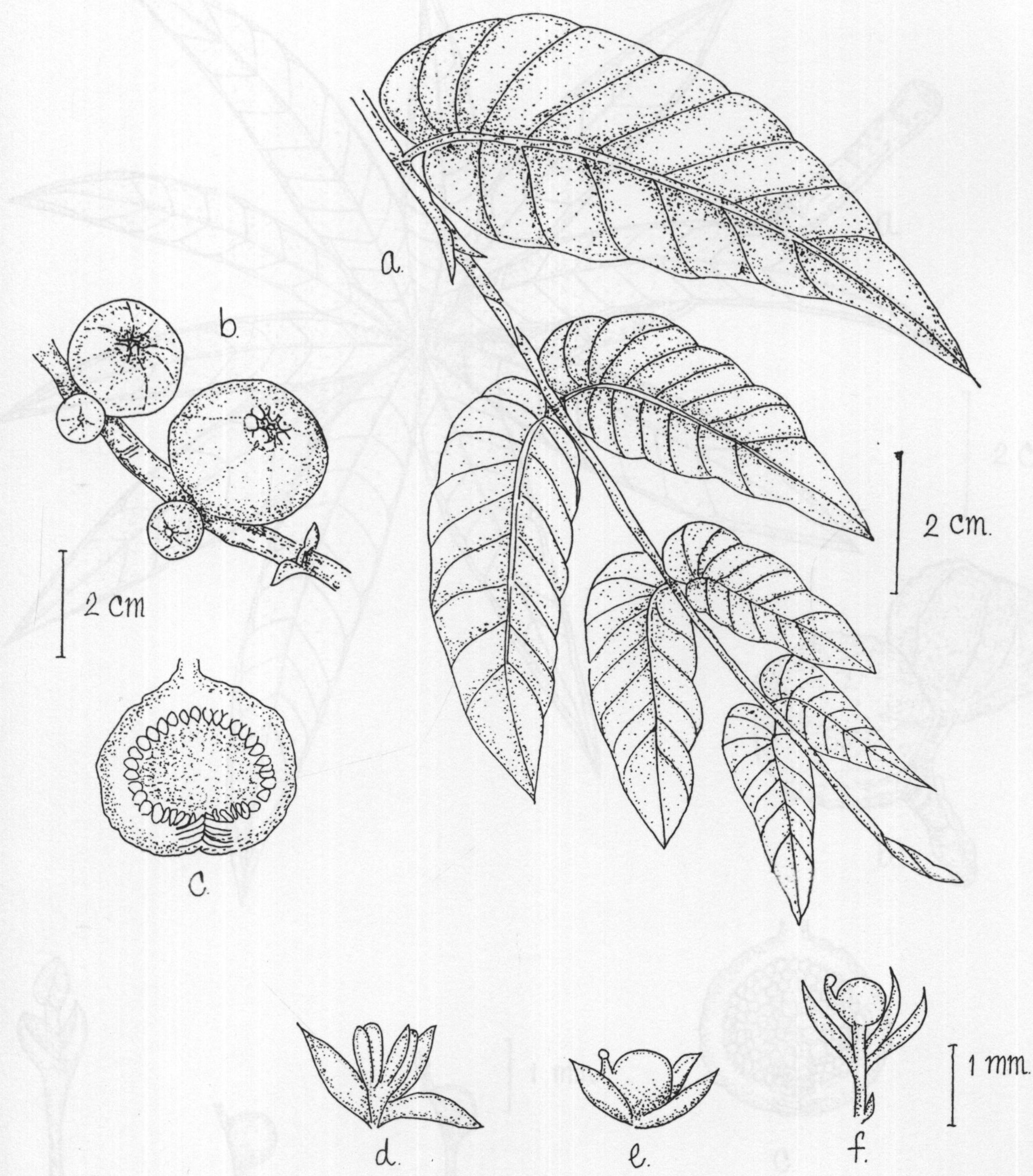


Figure 4.27 *Ficus semicordata* Buch.-Ham. ex Sm.; a. leaves, b. figs, c. long section of syconium, d. male flower, e. gall flower, f. female flower (seed)

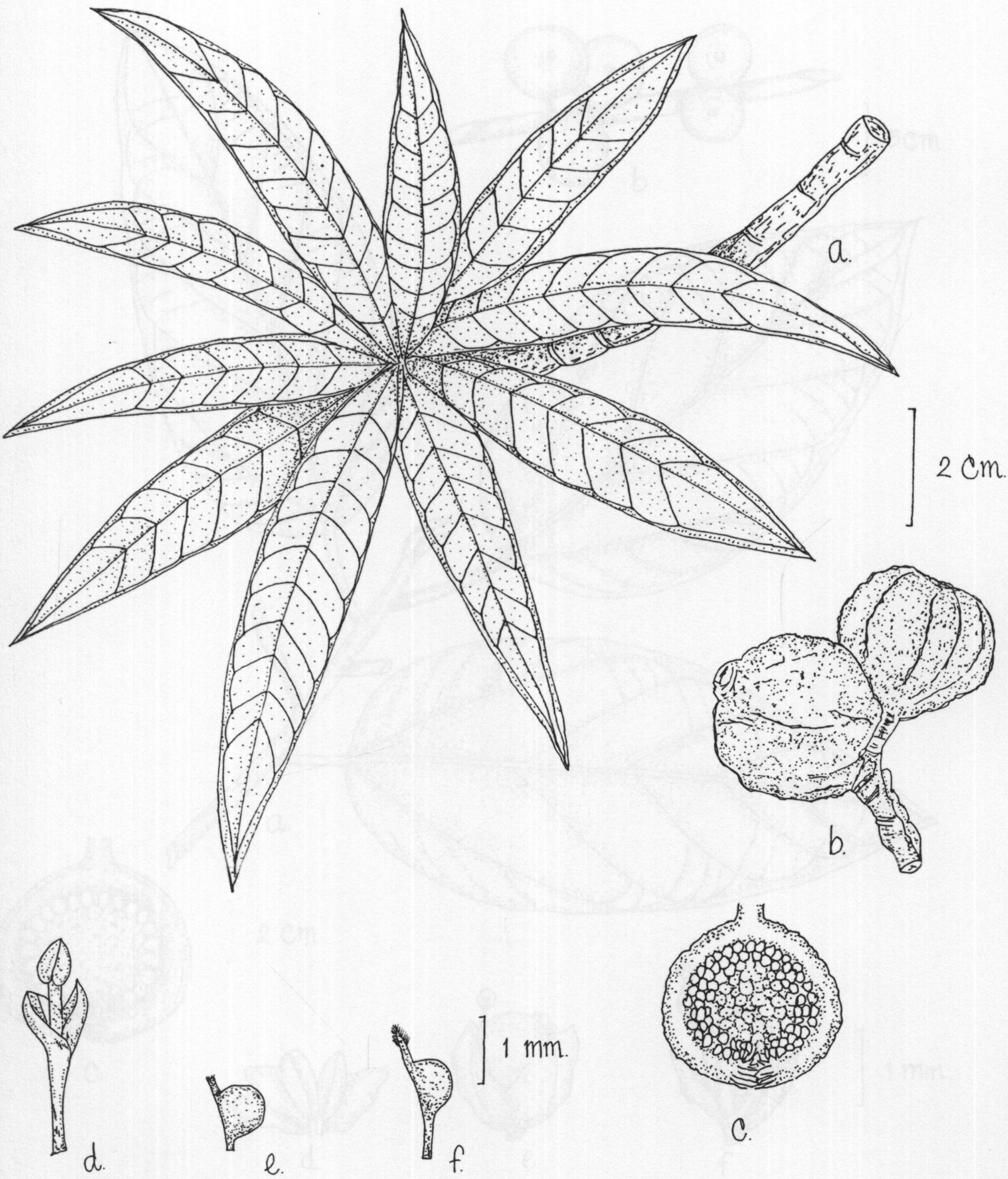


Figure 4.28 *Ficus squamosa* Roxb.; a. leaves, b. figs, c. long section of syconium, d. male flower, e. gall flower, f. female flower (seed)

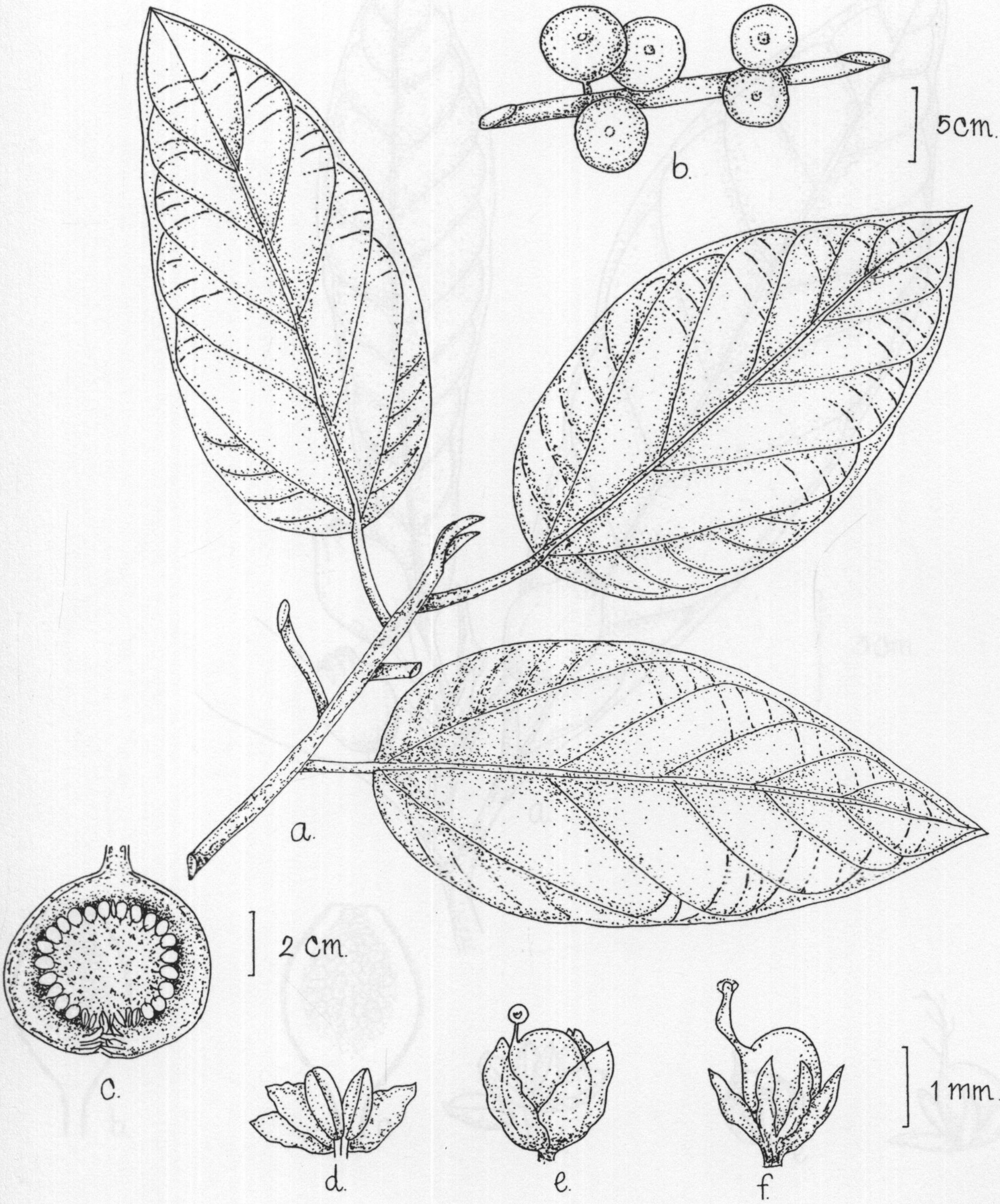


Figure 4.29 *Ficus variegata* Blume; a. leaves, b. figs, c. long section of syconium, d. male flower, e. gall flower, f. female flower (seed)

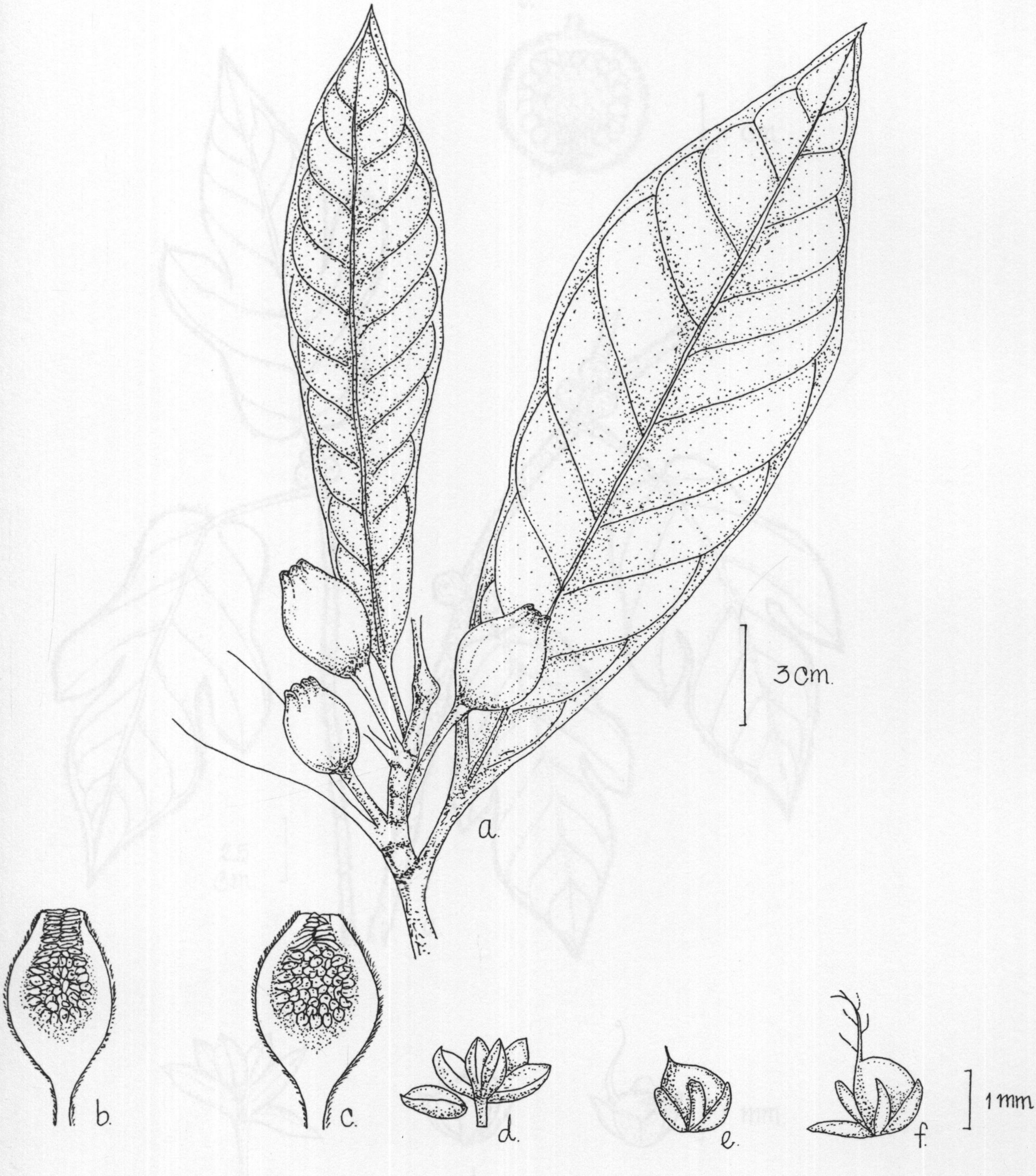


Figure 4.30 *Ficus ischnopoda* Miq.; a. fruiting branch, b. long section of male syconium, c. long section of female syconium, d. male flower, e. gall flower, f. female flower (seed)

Figure 4.31 *Ficus hirta* Vahl.; a. fruiting branch, b. long section of male syconium, c. male flower, d. gall flower, e. female flower (seed)

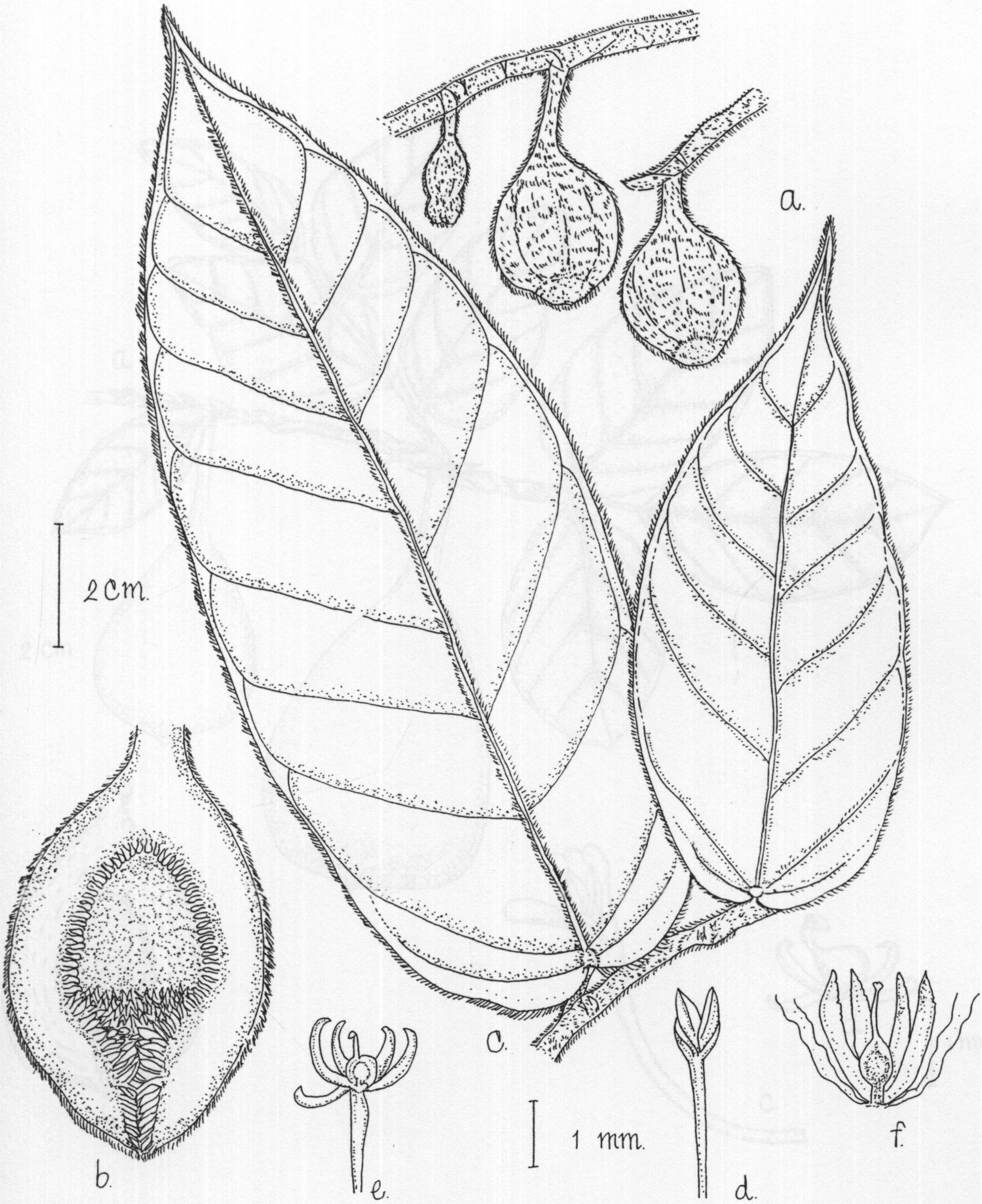


Figure 4.32 *Ficus anserina* Corner; a. fruits, b. long section of male syconium, c. leaves, d. male flower, e. gall flower, f. female flower (seed)

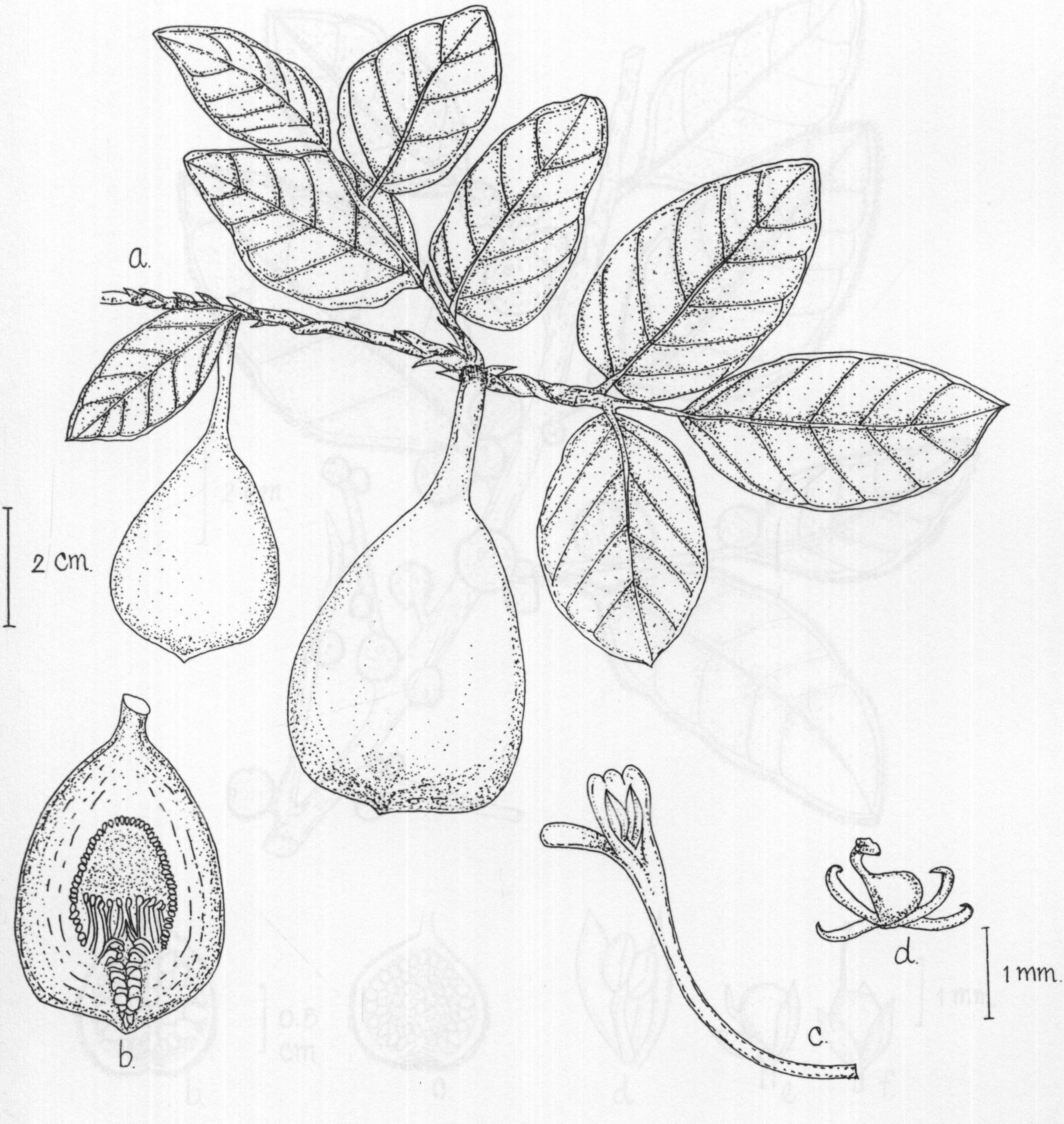


Figure 4.33 *Ficus pumila* L.; a. fruiting branch, b. long section of male syconium, c. male flower, d. gall flower

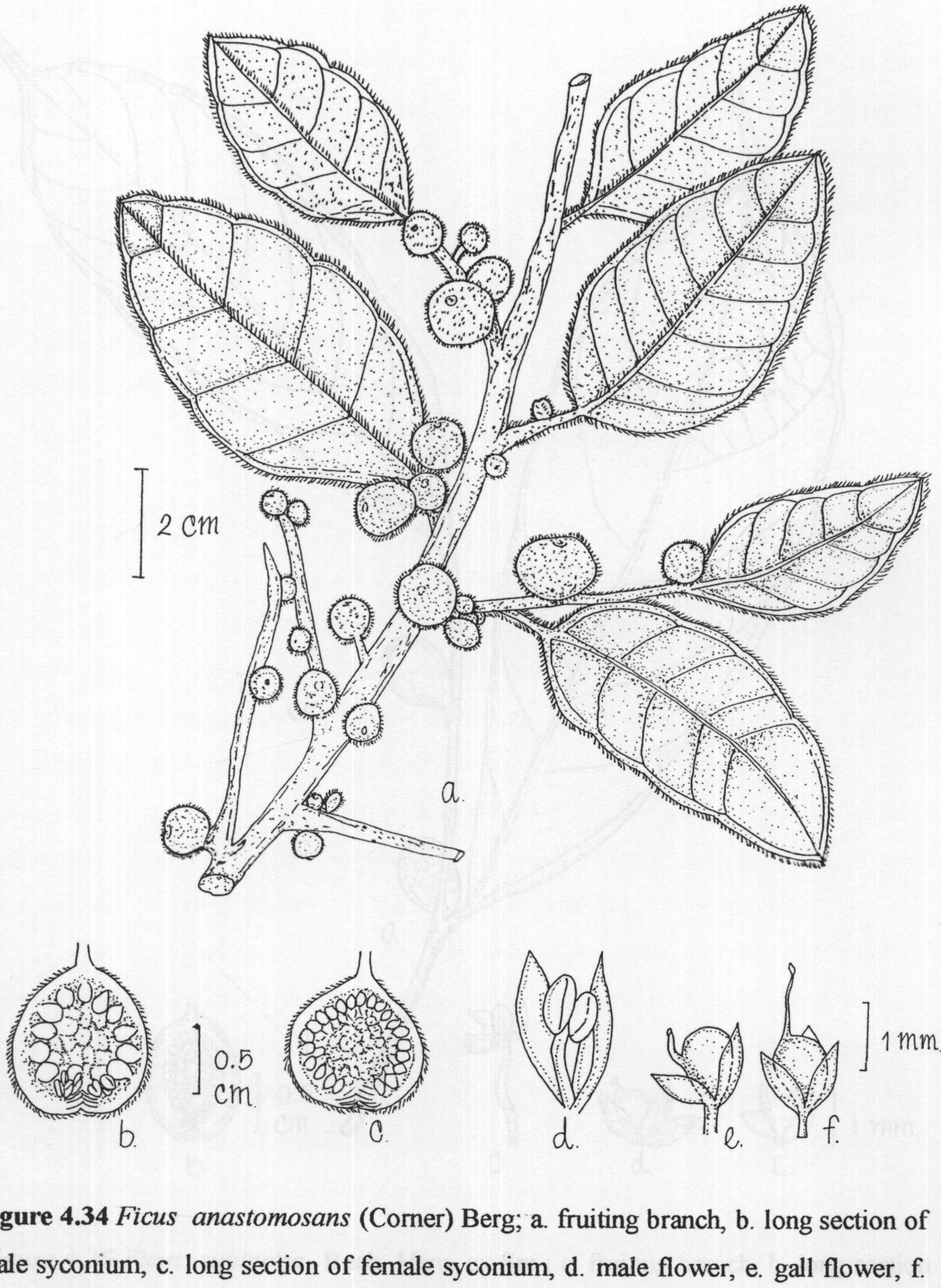


Figure 4.34 *Ficus anastomosans* (Corner) Berg; a. fruiting branch, b. long section of male syconium, c. long section of female syconium, d. male flower, e. gall flower, f. female flower

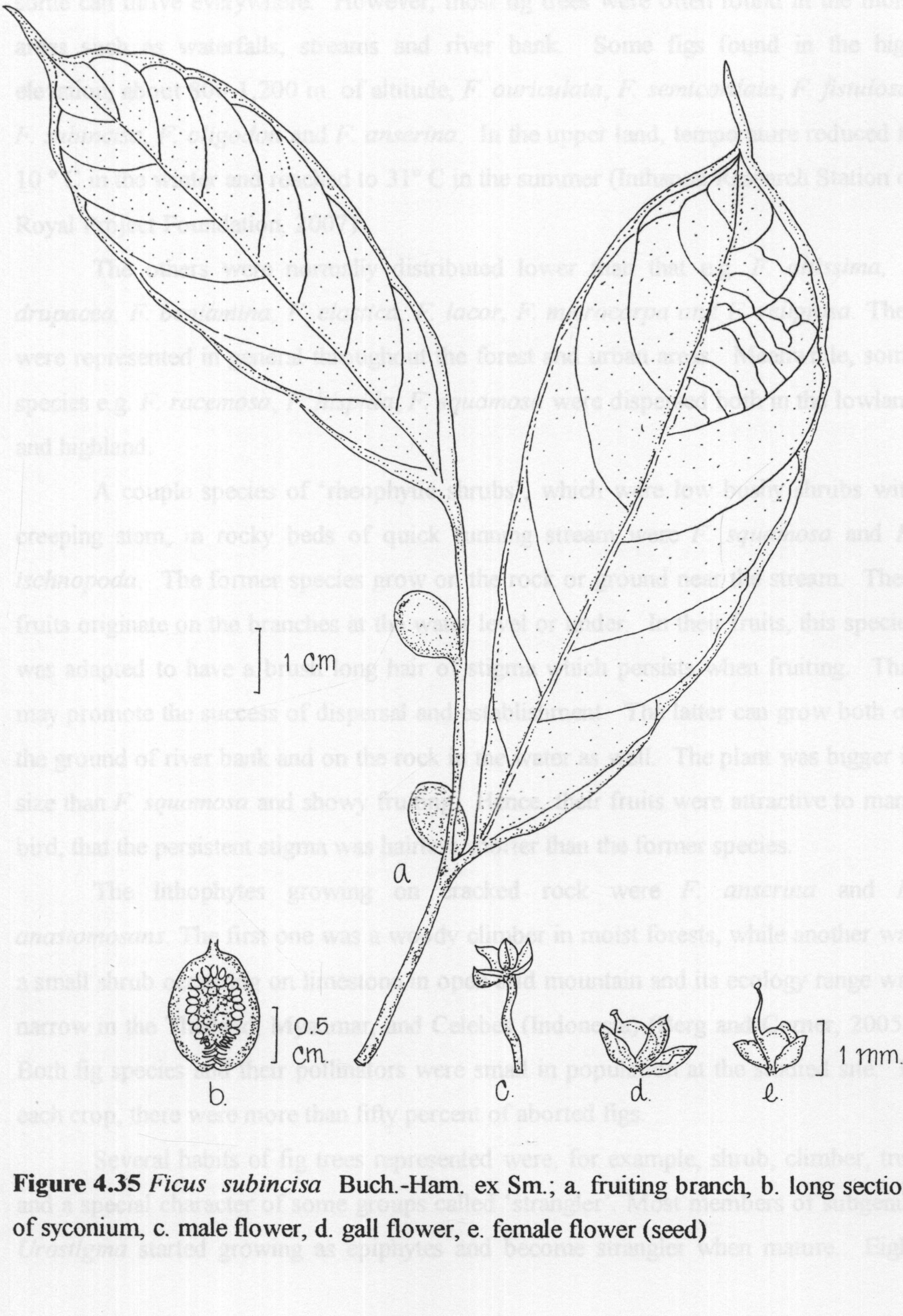


Figure 4.35 ***Ficus subincisa*** **Buch.-Ham. ex Sm.; a. fruiting branch, b. long section of syconium, c. male flower, d. gall flower, e. female flower (seed)**

4.5 ECOLOGY AND DISTRIBUTION

The fig trees were found from 310 to 1,200 m asl. The native and cultivated plants occurred in different habitats. Some species survive in unique habitats, whereas some can thrive everywhere. However, most fig trees were often found in the moist areas such as waterfalls, streams and river bank. Some figs found in the high elevation, about 800-1,200 m. of altitude, *F. auriculata*, *F. semicordata*, *F. fistulosa*, *F. subincisa*, *F. oligodon* and *F. anserina*. In the upper land, temperature reduced to 10 ° C in the winter and reached to 31° C in the summer (Inthanon Research Station of Royal Project Foundation, 2007).

The others were normally distributed lower than that e.g. *F. altissima, F drupacea, F. benjamina, F. elastica, F. lacor, F. microcarpa and F. religiosa.* They were represented in general throughout the forest and urban areas. Meanwhile, some species e.g. *F. racemosa*, *F. hispida*, *F. squamosa* were dispersed both in the lowland and highland.

A couple species of 'rheophytic shrubs', which were low bushy shrubs with creeping stem, in rocky beds of quick running stream were *F. squamosa* and *F. ischnopoda*. The former species grow on the rock or ground near the stream. Their fruits originate on the branches at the water level or under. In their fruits, this species was adapted to have a brush long hair of stigma which persists when fruiting. That may promote the success of dispersal and establishment. The latter can grow both on the ground of river bank and on the rock in the water as well. The plant was bigger in size than *F. squamosa* and showy fruiting. Hence, their fruits were attractive to many bird, that the persistent stigma was hairless shorter than the former species.

The lithophytes growing on cracked rock were *F. anserina* and *F. anastomosans*. The first one was a woody climber in moist forests, while another was a small shrub occurring on limestone in open arid mountain and its ecology range was narrow in the Thailand, Myanmar, and Celebes (Indonesia) (Berg and Corner, 2005). Both fig species and their pollinators were small in population at the studied site. In each crop, there were more than fifty percent of aborted figs.

Several habits of fig trees represented were, for example, shrub, climber, tree and a special character of some groups called 'strangler'. Most members of subgenus *Urostigma* started growing as epiphytes and become strangler when mature. Eight species were both natural and cultivated plants including *Ficus altissima*, *F. benjamina*, *F. lacor*, *F. microcarpa*, *F. religiosa*, *F. superba* var. *japonica*, *F. callosa* and *F. hispida*.

Their pollinators were mostly found in each fig specimens except 5 species, i.e. *F. curtipes*, *F. rumphii*, *F. pumila*, *F. maclellandii* and *F. anserina*, that only flower and fall. The common species of monoecious were *F. benjamina*, *F. lacor*, *F. religiosa* and *F. racemosa*. They were strangler plants that were mainly birds' food and usually dispersed by them. Except the last species, *F. racemosa*, that its fruits are usually preserved by some small mammals such as squirrels, fruit eating bats and insect- eating birds. Hence, its seedling occasionally found under its crown or at the river bank.

The number of flowering and fruiting times are diverse in each fig tree. The shorter one is only a time a year and it can be 5-6 times in some species such as *F. racemosa* and *F. hispida* (Table 4.2). Both species can release the large number of fig wasps in each crop.

Table 4.2 The characters, habits and appearance of *Ficus* and their pollinators in Chiang Mai during June 2005-May 2007.

No	*Ficus* species	Sexual system	Pollinators present?	Habits	Crop / year
1	*F. altissima* Bl.	M	Yes	E /T	1-2
2	*F. benjamina* L. var. *benjamina*	M	Yes	E /T	2-3
3	*F. benjamina* var. *nuda* (Miq.) Barrett.	M	Yes	E /T	2-3
4	*F. curtipes* Corner	M	No	E /T	1
5	*F. drupacea* Thunb.	M	Yes	T	1
6	*F. elastica* Roxb.	M	Yes	E/T	1
7	*F. lacor* Ham.	M	Yes	E /T	1
8	*F. maclellandii* King	M	Yes	T	1-2
9	*F. microcarpa* L.f.	M	Yes	E /T	1-2
10	*F. religiosa* L.	M	Yes	E /T	1-2

Table 4.2 The characters, habits and appearance of *Ficus* and their pollinators in Chiang Mai during June 2005-May 2007. (continued)

No	*Ficus* species	Sexual system	Pollinators present?	Habits	Crop / year
11	*F. rumphii* Bl.	M	No	E /T	1-2
12	*F. superba* Miq. var. *japonica* Miq.	M	Yes	E /T	1
13	*F. callosa* Willd.	M	Yes	T	1-2
14	*F. racemosa* L. var. *racemosa*	M	Yes	ST	5-6
15	*F. racemosa* var. *miquelli* (King) Corner	M	Yes	ST	5-6
16	*F. auriculata* Lour.	D	Yes	ST	1-2
17	*F. fistulosa* form1, form2	D	Yes	ST	1-2
18	*F. hispida* var. *hispida* L.f.	D	Yes	ST	5-6
19	*F. hispida* var. *badiostrigosa* Corner	D	Yes	ST	5-6
20	*F. oligodon* Miq.	D	Yes	T	1-2
21	*F. semicordata* Buch.-Ham. ex J. E. Sm.	D	Yes	ST	2-3
22	*F. squamosa* Roxb.	D	Yes	R/L	2-3
23	*F. variegata* Blume	D	Yes	T	1-2
24	*F. ischnopoda* Miq.	D	Yes	R/L	2-3
25	*F. hirta* Vahl	D	Yes	S	2-3
26	*F. anserina* Corner	D	No	C/L	1-2
27	*F. pumila* L.	D	No	C	2-3
28	*F. anastomosans* (Corner) Berg	D	Yes	C/L	2-3
29	*F. subincisa* Buch.-Ham. ex Smith	D	Yes	S	2-3

M= monoecious, D=dioecious, E= epiphytes, T= tree, S= shrub, ST= small tree, C= climbing, R, = rheophytes, L= lithophytes

4.6 DISCUSSION AND CONCLUSION

The publications of taxonomic study on figs in Thailand are still a few numbers. In this study, the neighbors' floras were used.

Twenty-six fig species found in the study sites, Chiang Mai. Most of the fig trees had their specific pollinators, except *Ficus auriculata* and *F. oligodon* that shared the same species of *Ceratosolen emarginatus* Mayr as the pollinator. The pollinators of *F. curtipes, F. rumphii, F. pumila, F. maclellandii* and *F. anserina* could not be found in the survey

The widespread fig species usually possessed a large number of individuals of pollinators. However, the number varied in each season. The figs with a small number of fig wasp populations were *F. ischnopoda* and *F. subincisa*. Many figs aborted in a few weeks. It might be as a result of the small population of the fig trees in the wild. The ripen fruits of *F. racemosa* was served many kind of animals so that they can distribute lots of seedling. Number and size of figs in each crop was one of the reasons to promote them. However, some fig species produced a small size such as *F. benjamina*, but the large number of their figs attracted many kinds of bird, which help them planting new generation, also the same as *F. microcarpa* and *F. lacor*.

Sometimes the complication caused by local name of the plant, e.g. fig tree that we call 'Sai' in Thai is the one of sacred tree that the people avoid to cut down, indeed many figs in *Urostigma* usually name to 'Sai' such as *F. benjamina*, *F. macrocarpa*, *F. curtipes*, *F. maclellandii*. Another pair of missing usually occurs between *F. religiosa* 'Pho' and *F. rumphii* 'Pho khi nok' that people often have wrong selecting to plant.

The population of the fig pollinators was diverse in each fig species. The widespread fig species usually present a large number of their pollinators. However, they were different occurred in each season. For instance, *F. racemosa*, the production of pollinator offspring was higher in dry season (January and November) than rainy season (Wang *et al.*, 2005, and our observation). The fig with less number of fig wasp population were *F. anserina*, *F. subincisa* and *F. anastomosans*, many figs failed without entering. The results may be the small population fig trees in the wild. Besides the pollinators, that effect to size of both populations, their dispersal carriers was also the important factor. The results showed that the animal attractive figs usually success to disperse and get more new generation.

There were diverse types of fig tree characters represented such as leaf shape and syconium. However, within the species of dioecious fig, male and female figs always present the same characters in the wild. For the study of their morphology, it difficult to separate male from female tree until their syconium occurred.

The ripen fruits of many figs served many kind of animals so that they can distribute lots of their seedling. Some figs produced a large number of seeds in each crops and success to distribute in nature such as *F. racemosa*, *F. hispida* and *F. auriculata*. Whereas, some figs have small size of syconium as well as produce not many seeds.

In order to complete the knowledge of fig biology and classification, future studies on the details of interaction between figs and fig wasps should be of valuable works. It would be support the knowledge of fig diversity, distribution and also conservation of natural ecosystem.

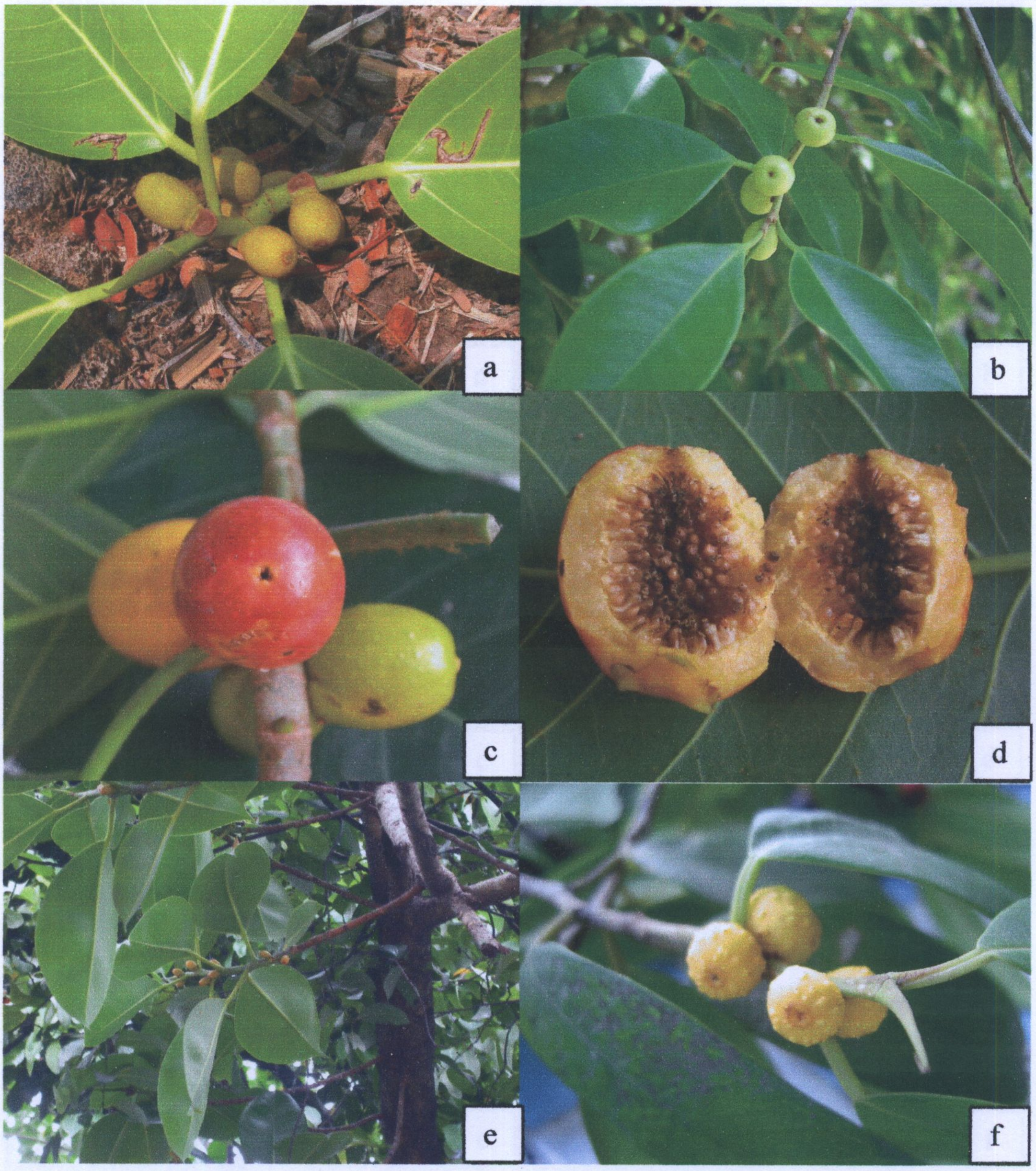


Figure 4.36 Some figs in subgenus *Urostigma*; *a. F. altissima, b. F. benjamina, c. F. drupacea, d. F. drupacea* (long section), *e. F. elastica, f. F. maclellandii*

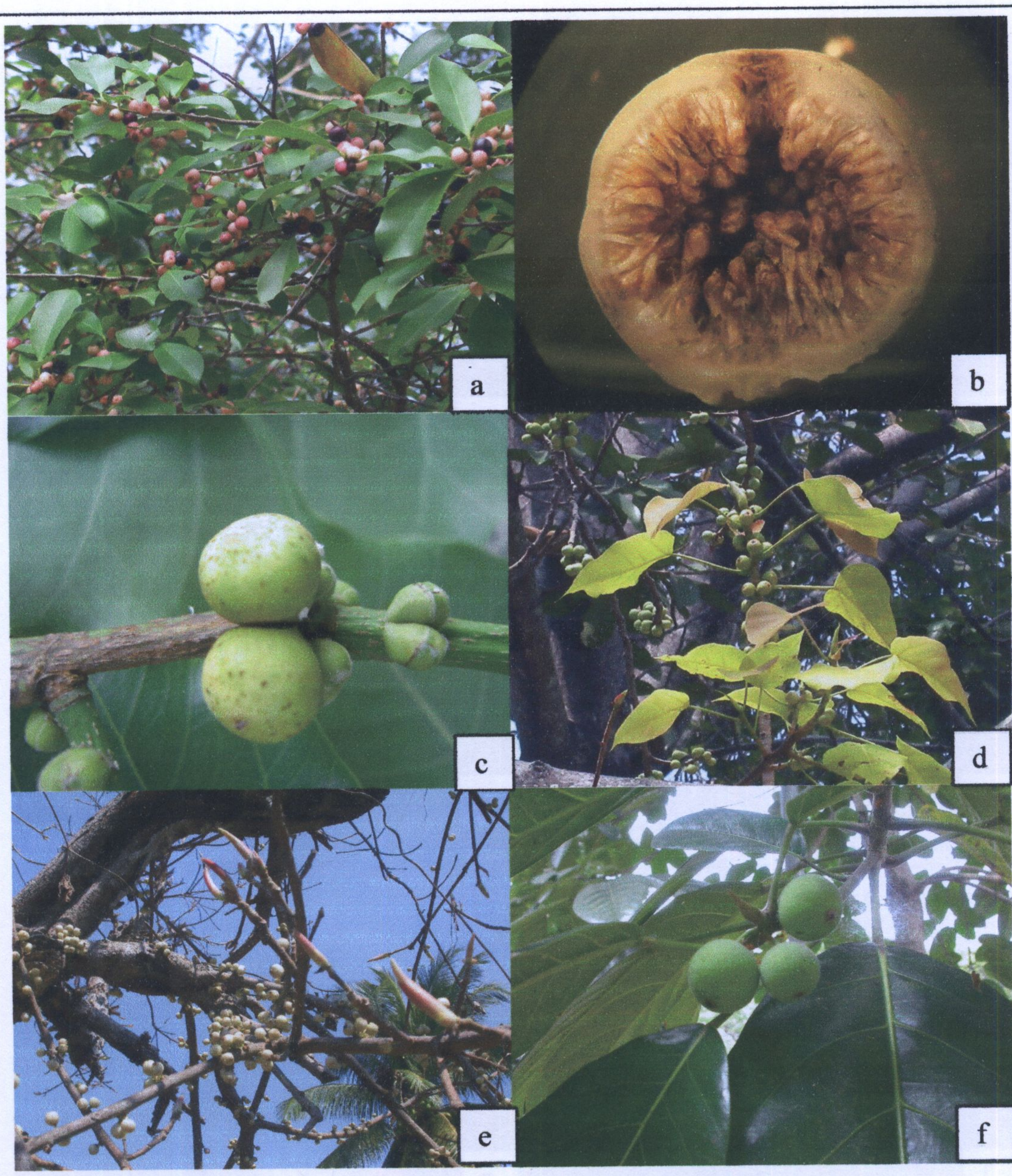


Figure 4.37 Some figs in subgenus *Urostigma*; *a. F. microcarpa, b. F. microcarpa (long section), c. F. religiosa, d. F. rumphii, e. F. superba* and subgenus *Pharmacosycea f. F. callosa*

Figure 4.38 Some figs in subgenus *Sycomorus*; *a. F. auriculata* (tree), *b. F. auriculata* (figs), *c. F. fistulosa* (fig), *d. F. fistulosa* (leaves), *e. F. squamosa* (fig), *f. F. squamosa* (leaves)

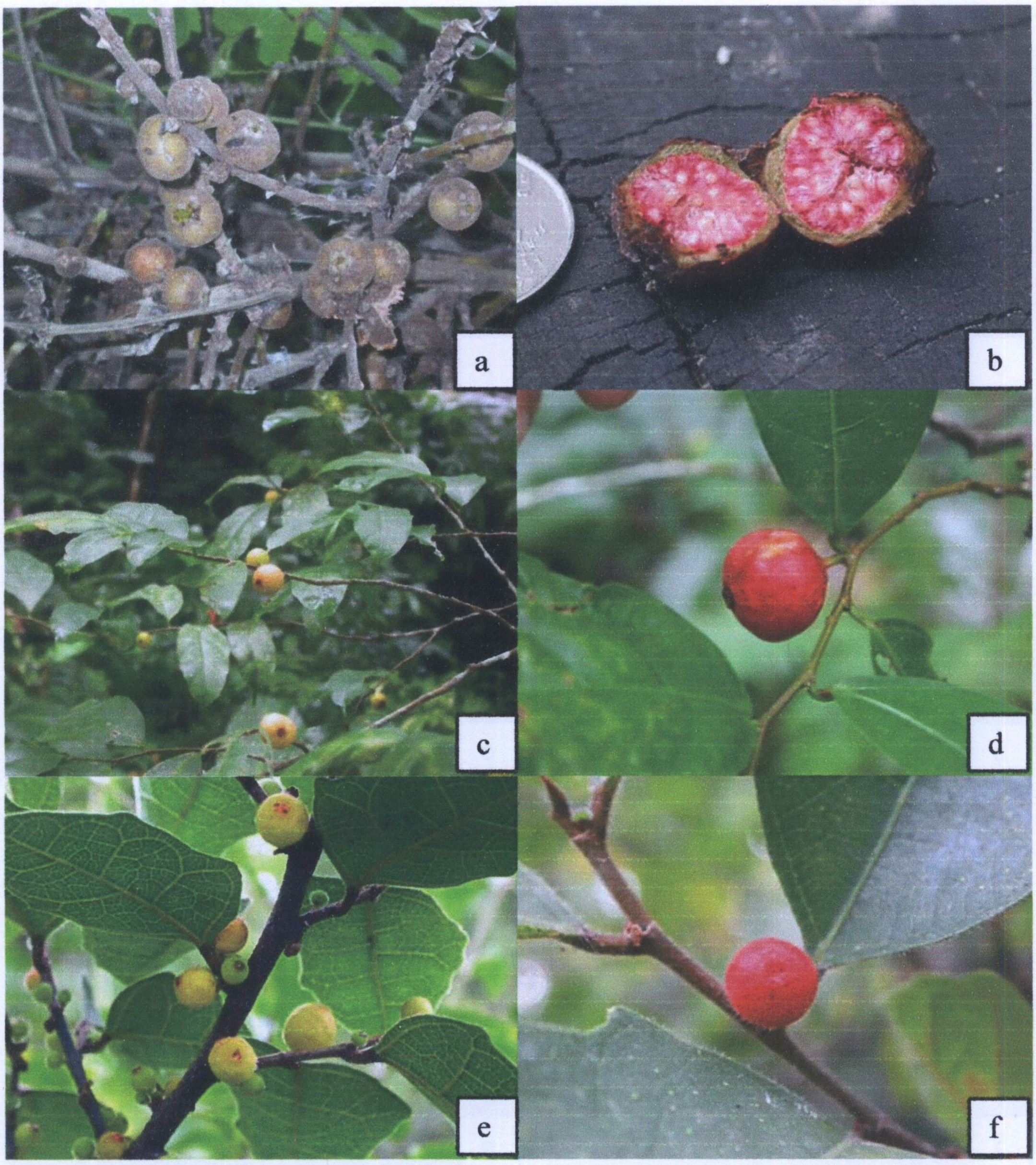


Figure 4.39 Some figs in subgenus *Sycomorus*; *a. F. semicordata*, *b. F. semicordata* (long section); subgenus *Sycidium*; *c. F. subincisa* (male), *d. F. subincisa* (female), *e. F. anastomosans* (male), *f. F. anastomosans* (female)

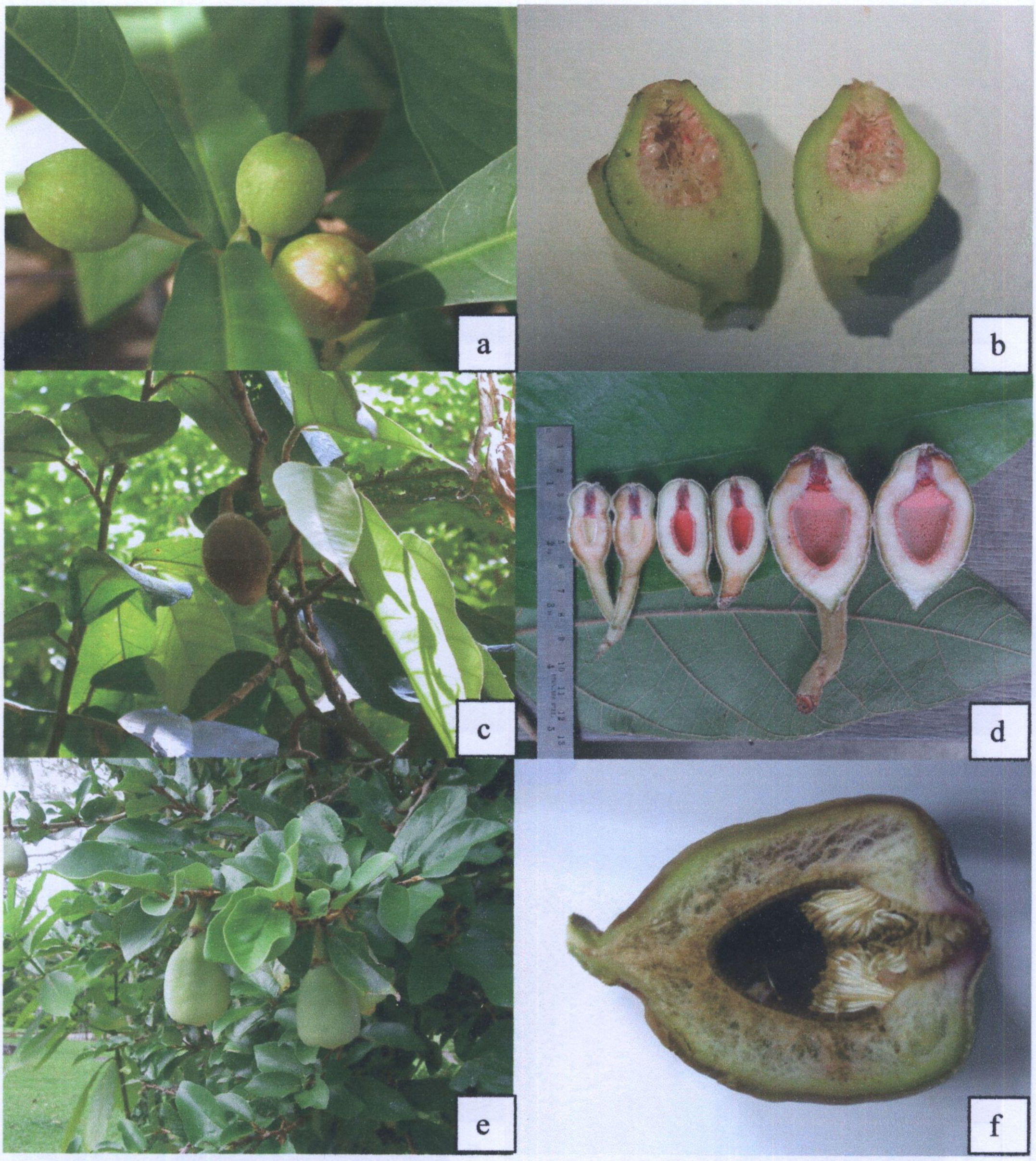


Figure 4.40 Some figs in subgenus *Ficus*; *a. F. ischnopoda*, *b. F. ischnopoda* (long section), subgenus *Synoecia; c. F. anserina*, *d. F. anserina* (long section), *e. F. pumila*, *f. F. pumila* (long section)

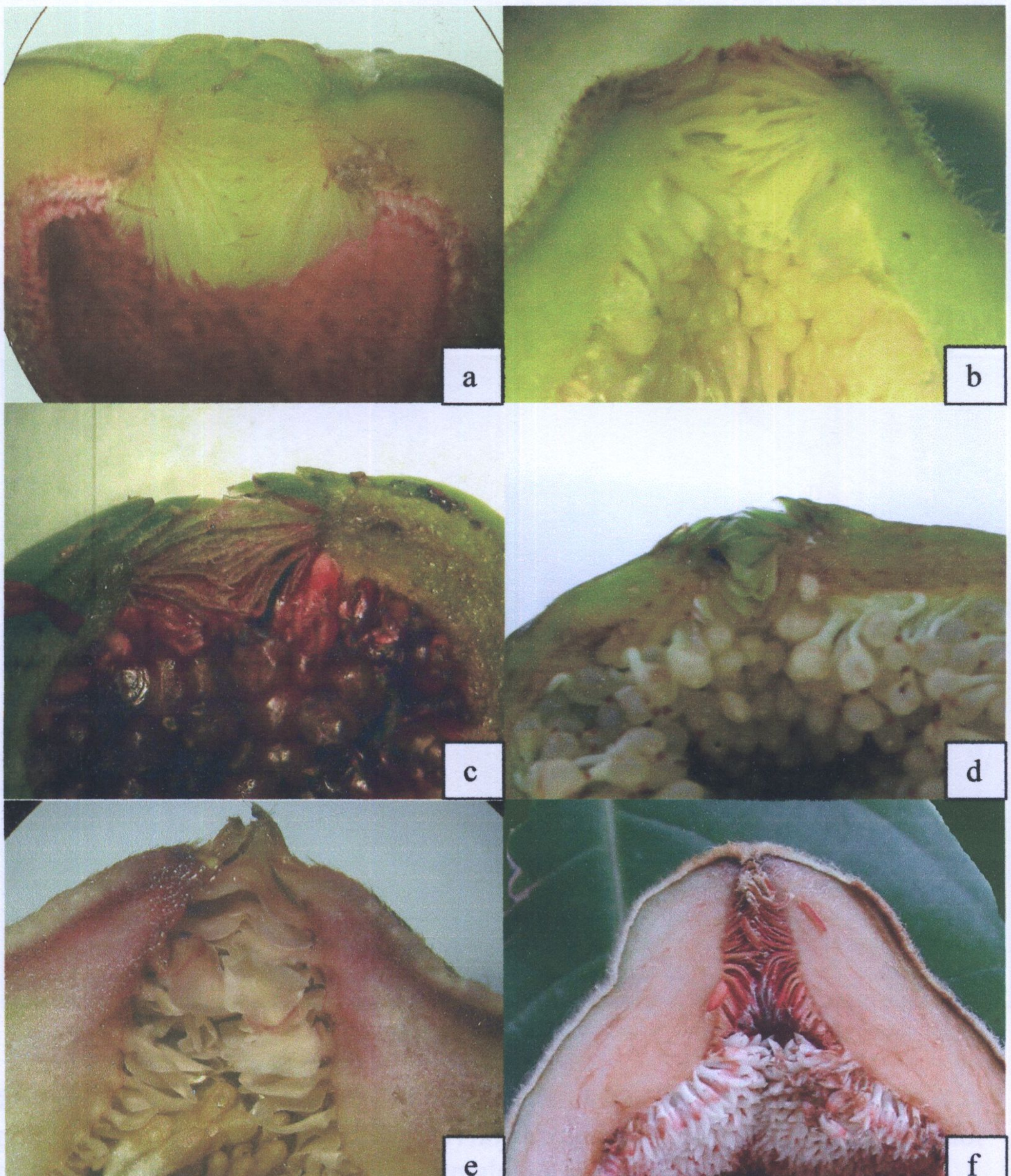


Figure 4.41 The variation of fig ostiolar bracts: *a. F. auriculata, b. F. ischnopoda, c. F. fistulosa, d. F. semicordata, e. F. pumila, f. F. anserina*

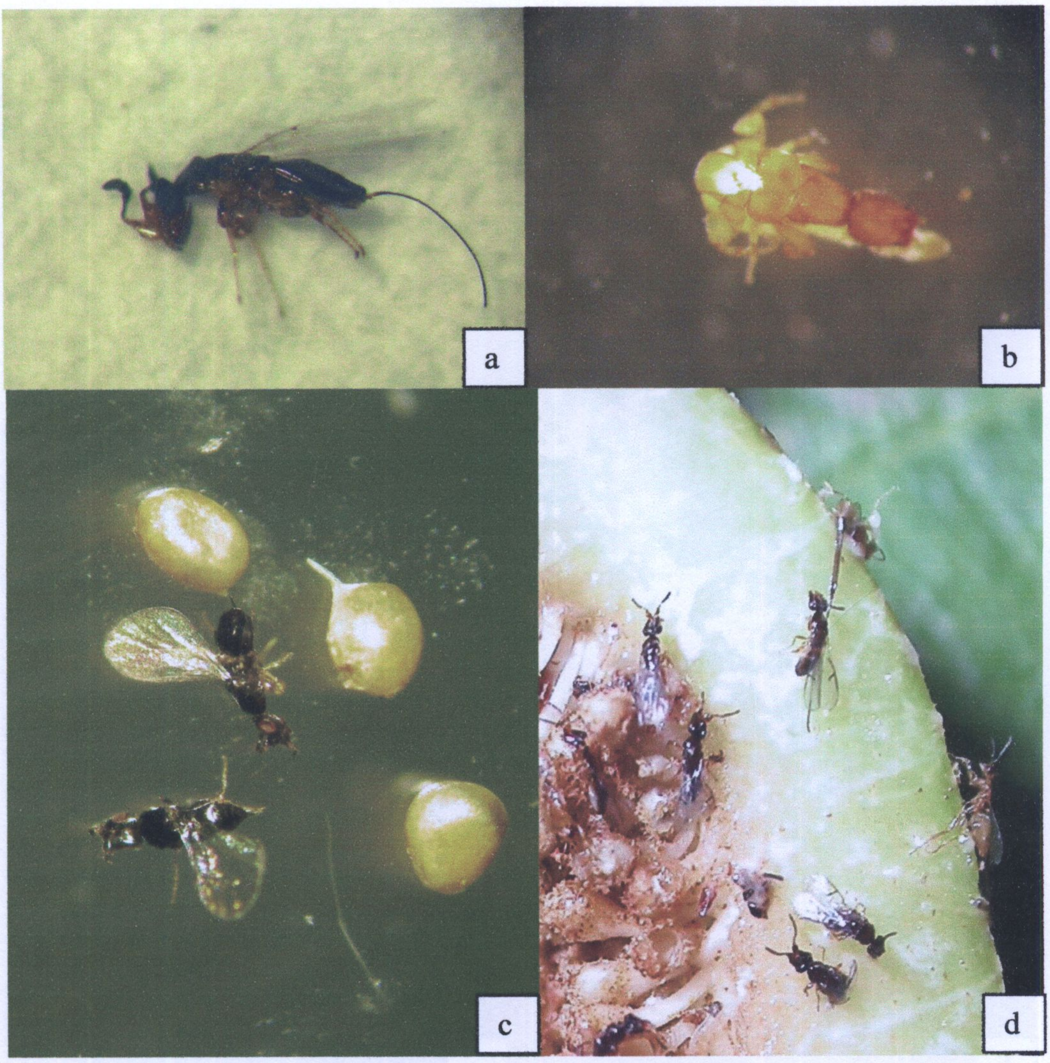


Figure 4.42 Some fig wasps: *Ceratosolen fusciceps; a.* female, *b.* male: pollinators of *F. racemosa, c. Liphorrhophalum* sp. (female), female pollinator of *F. anastomosans, d. C. solmsi.*, female pollinator of *F. hispida*

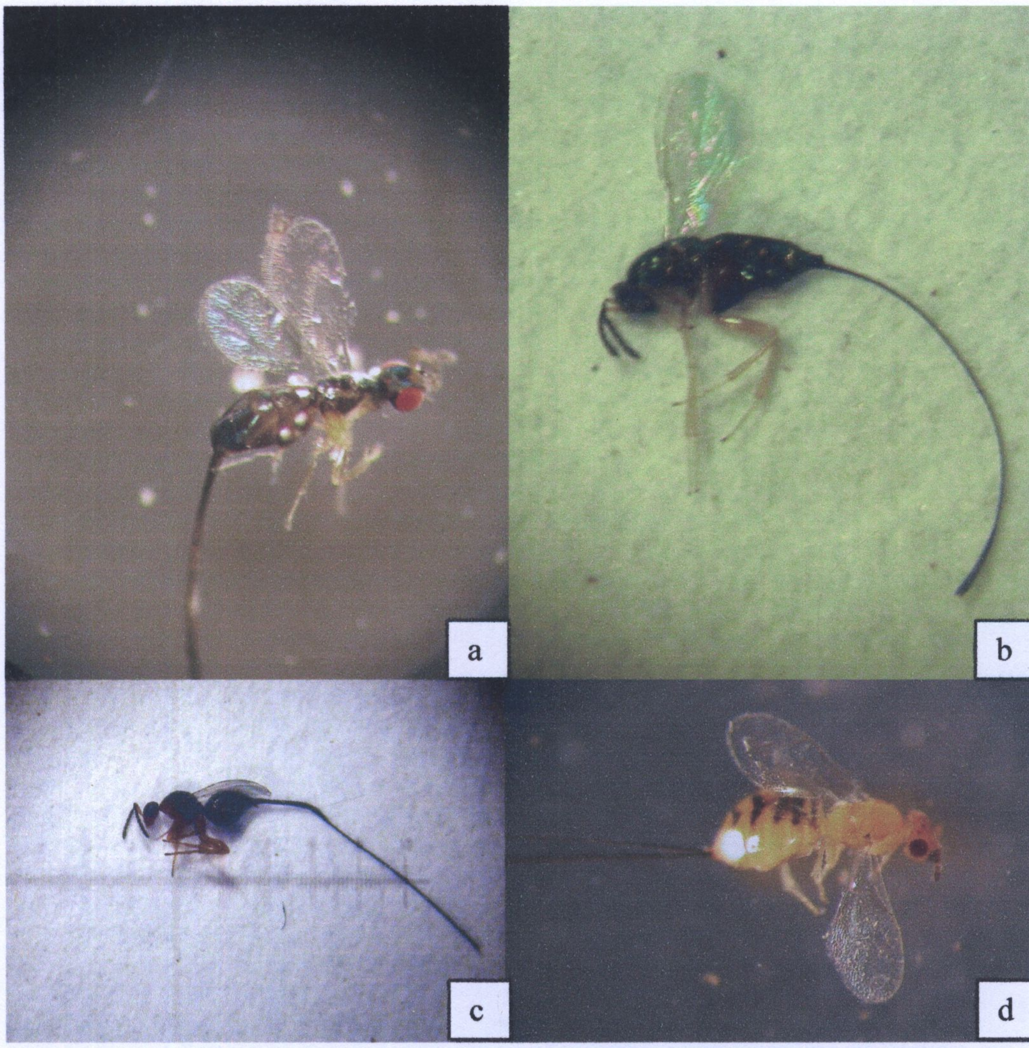


Figure 4.43 Some female non pollinating wasps:
a. Apocrypta sp1, *b. Apocrypta* sp2, *c. Philotrypesis* sp., *d. Platyneura* sp. (*Apocryptophagus*)

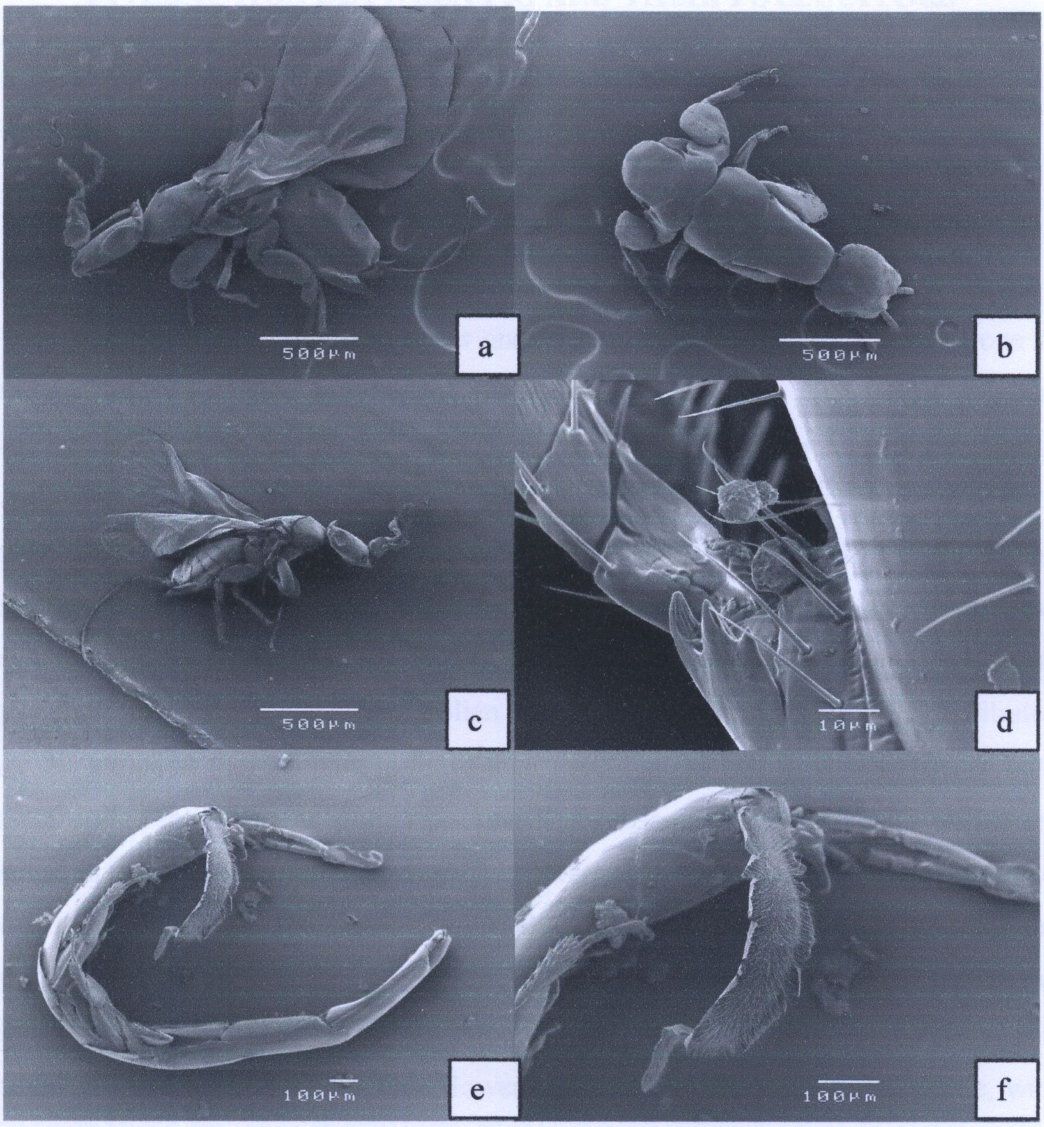


Figure 4.44 The illustrations of some fig wasps under SEM: *Ceratosolen fusciceps*, *a.* male, *b.* female: *Eupristina* sp., *c. female*, *d. female with pollen grains*: *Platyneura* sp., *e.*, *f.* male

CHAPTER V

INTERACTION BETWEEN FIG AND THEIR POLLINATORS

5.1 DIOECIOUS FIGS

The benefits of pollination for a fig wasp

5.1.1 Introduction

The relationship between *Ficus* and their highly specific pollinators is one of the best-studied obligate mutualisms (Bronstein and McKey, 1989; Kjellberg and Maurice, 1989; Berg and Wiebes, 1992). There are over 750 fig species distributed mainly in the tropical areas, each of which is associated with one or more species of highly specialized pollinator fig wasps (Bronstein and McKey, 1989; Cook and Rasplus, 2003). Adult female pollinators (foundresses) deposit pollen in figs at about the same time as they attempt to lay their eggs in the flowers and gall them. Pollination may be passive, where pollen from numerous male flowers is distributed over the wasps as they prepare to leave their natal figs, or active, where females both collect pollen into thoracic pollen pockets and subsequently 'paint' with pollen the stigmas inside receptive figs that they have entered. Active pollination is likely to be much more efficient at transferring pollen than passive pollen, and reflecting this the ratio of male to female flowers inside figs is generally a good predictor of the pollination method of the wasps (Kjellberg *et al.*, 2001). Fig wasp behavior and associated plant traits, such as male flower numbers, appear to be highly labile, with frequent gains and losses of active pollination behavior (Kjellberg *et al.*, 2001; Cook *et al.*, 2004).

Monoecious fig species produce both seeds and pollen-carrying fig wasps, whereas functionally dioecious fig trees have female plants that produce only seeds and male plants that produce both pollen and the pollinator wasps to disperse it (Bronstein and McKey, 1989; Nefdt and Compton, 1996). The former produce only seeds because, after attracting the pollinators, they prevent them from ovipositing.

Female figs achieve this by having female flowers with much longer styles than those in male figs, and there are also differences in the structure of the stigma, making ovipositor penetration more difficult. Jousellin *et al.* (2003) showed that pollinator species can benefit from active pollination of figs, probably because larval survivorship is higher in fertilized seeds. Benefits were less clear for passively-pollinating species.

For dioecious fig, one of the wild species, *Ficus montana* Burm.f., was selected. The fig tree population in glasshouse was examined so the fig trees could be closely monitored. The studies similarly examined whether the females that carry pollen into male figs of *F. montana* are at a reproductive advantage in relation to those that do not. This fig tree species is unusual in that plants have figs with a wide range of male flower numbers, encompassing the range that is typical of both actively and passively pollinated *Ficus* species (Suleman and Raja, unpublished). By preventing fig wasps from ovipositing after entry into receptive figs, another examination was whether the absence of seed production in the male figs of this species reflects a physiological inability to develop seeds and whether pollen carrying into male figs is sufficient to stimulate their further development.

5.1.2 Literature review

F. montana Burm.f. is one of the member of *Sycidium* section in the subgenus *Sycidium* (Berg 2003b; Noort and Rasplus, 2005) It has well-developed pistillodes in staminated flowers. In several species, the 'staminate' flowers even have pistils similar to the short-styled pistillate flowers and can be regarded as (morphologically) bisexual. For the ostiolar bract, this section has developed it differently from other groups that the lack distinct bracts (Berg, 1989).

This fig species distributes in South East Asia. It is a small climbing shrub, 1-3 m high with alternate leaves and small oval syconium. Its distribution is in limestone mountains in moist forests (Berg and Corner, 2005). Its flowering is about 4-6 times annually. Most of *Sycidium* section have pollinators in the genus *Kradibia*, except *F. montana*, of which its pollinators is *Liporrhopalum* (Berg, 2005). The characters of *F. montana* were described as follows (Berg, 2003b);

***Ficus montana* Burm. f.** Subgenus *Sycidium*

Shrub: 1-3 m tall; **Leaf**: spiral, alternate, margin of the lamina coarsely crenate-dentate to subentire; base of the lamina cuneate to rounded; basal lateral vein up to 1/2-1/3 of the length of the lamina; waxy glands confined to the axils of the basal lateral veins; leafy twig and laminas (densely or sparsely), whitish hair or indumentum absent, hair straight, curved or $\pm$ crinkled, leafy twig usually hollow; epidermis of the petiole persistent. **Figs**: axillary or just below the leaves; in pairs or solitary; figs usually with distinct peduncle (0.1)-0.2-0.8 cm long; ostiole c. 1 mm diam., surrounded by a sublobate rim; fruit (or endocarp body) distinctly tuberculate; stipule up to 1-1.2 cm long, subovate to lanceolate and chartaceous, not striate, cauducous. **Male flowers**: near apical pore; stamens 2; anthers oblong. **Gall flowers**: calyx lobes 4 or 5, linear-lanceolate; style lateral, short. **Female flowers**: basal bracteole 1; calyx lobes 4 or 5; ovary ovoid-ellipsoid; style lateral, long; stigma cylindric, shallowly 2-lobed. Achenes broadly ovoid, apically slightly concave on one side, with ± small tubercles. **Flowering and Fruiting** year-round.

The specific pollinator is *Liporrhopalum tentacularis* (Grandi). It was described by Wiebes (1994) as follow;

Liporrhopalum tentacularis (Grandi)

The female head is subquadrate, with protruding eyes; the cheek is nearly equal to the length of the eye. The antennae is very long: when reflexed over the body. The apical segment projects posterior to the gaster; the numberous sensilla are very short and hooked, interspersed with many setae. The mandible is bidentate, and it has one gland; the appendage bear four or five ventral lamellae; the maxilla has a distinct bacilliform process. The total length is 1.4-1.5 mm; the vales of the ovipositor are one-quarter to one-third of the length of the gaster.

The male head is almost triangular in outline, because it is rather wide posteriorly: 1 ½ times as wide as it is long; the eyes are quite large, equal in length to the cheek, and ca. one-seventh of the length of the head. The antennal scrobes are slightly exposed anteriorly and separated by a narrow, three-pointed clypeus. The mandible is tridentate, and it has two glands.

The pronotum has a large, strongly curved collar, and the posterior corners are tapering; the metanotal plates are distinctly contiguous. The fore tibia bears three dorso-apical teeth. The total length is ca. 0.8 mm.

The abortion hypothesis

This hypothesis suggested that fig tree abort figs that contain a very high proportion of wasp larvae (Janzen 1979; Axelrod and Hamilton 1981; Murray 1985 in Katharia-Gupta, 1999). Nefdt (1989) reported the experiments with pollen-free wasp of *F. burtt-davyi* (monoeciuos fig) some of larva could survive and some non-pollinator fig wasps developed in seed-free monoecious figs.

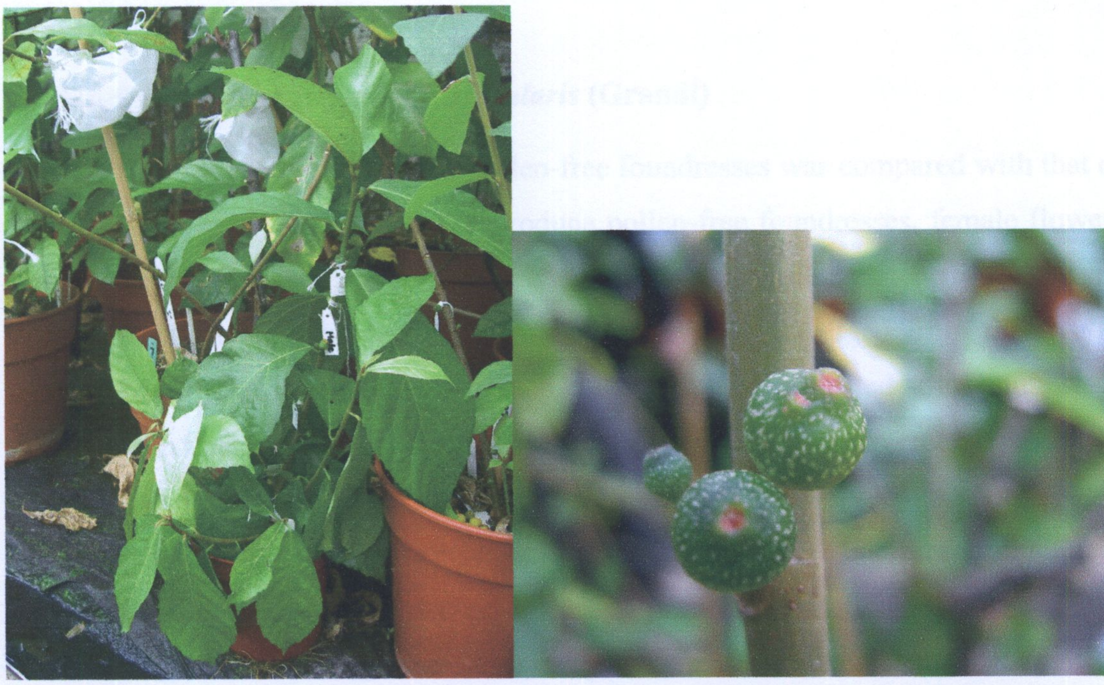
Furthermore, comparison between wasp numbers in aborted and unaborted figs showed no difference between the two (Bronstein, 1988). Male figs in dioecious species complete development without producing seeds. However, it may be possible that some of the ovaries harbouring wasp offspring in heavily exploited figs were aborted, giving rise to some of the vacant ovaries (bladders) observed in mature figs. All data available so far suggest that mostly pollinated figs reach maturity and abortion of figs was seen only under strong resource limitation (Bronstein, 1988).

5.1.3 Materials and methods

Species and study site

The University of Leeds glasshouse populations of *L. tentacularis* and *F. montana* (Figure 5.1) were used for two experiments that were carried out between November 2005 and June 2006.

The experiments were set to three times, the first one was carried out from November to December 2005, the second one was from January to March 2006 and the last one was from May to June 2006. Although the climate in the glasshouse was controlled, in the winter it was still cold (18-20 °C). In summer, the glasshouse was open. The average temperature in the period of the study was 21.1 °C (Table 5.1)



a. b.

Figure 5.1 *Ficus montana* Burm. f.; *a.* plant, *b.* fig (syconium)

Table 5.1 Temperature (ºC) of the University of Leeds glasshouse during the study from November 2005 to June 2006

Periods of the study	Mean max Temperature (ºC)	Mean min Temperature (ºC)	Average Temperature (ºC)
November 2005	20.0	16.3	18.1
December	21.3	18.8	20.0
January 2006	21.3	18.8	20.0
February	21.8	17.5	19.6
March	24.3	16.8	20.5
April	30.0	18.0	24.0
May	26.5	19.0	22.8
June	27.8	19.3	23.5
Mean	24.1	18.0	21.1

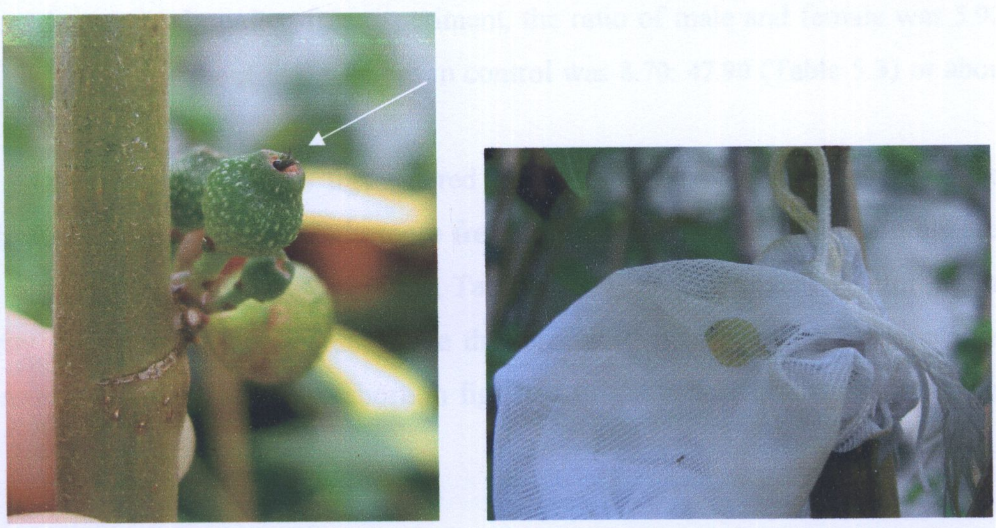
5.1.4 Experiment 1

Pollen-free of *Liporrhopalum tentacularis* (Grandi)

The reproductive success of pollen-free foundresses was compared with that of typical, pollen-carrying females. To produce pollen-free foundresses, female flowers in male figs that contained recently-mated female wasps were isolated from the male flowers shortly before the females would normally have emerged from their galls. Control foundresses were obtained from figs that had been collected at the same stage and placed in vials covered with a fine mesh. They were allowed to emerge as normal from the figs, and so would have had the opportunity to fill their pollen baskets.

Prior to this, 120 pre-receptive phase male figs had been enclosed in fine mesh bags while still attached to the trees, in order to prevent pollination. If the syconium became soft, it meant the figs start to be receptive. In a few hours later, they would be pollinated. Therefore, the hard fig would be selected.

Once at the receptive stage, 60 figs were allowed to be entered by a single pollen-free wasp and 60 by control wasps. This was achieved by placing the wasps at the ostioles using a fine paint brush (Figure 5.2).



a. b.

Figure 5.2 The female entering; *a.* some parts of wings and antenna left, *b.* the fig with entering female pollinator was bagged with the fine mesh bag

The treatment and control figs were located on the same plants. The bags were replaced after wasp's entry to prevent further pollinators entering, and also to prevent attacks by parasitic wasps. The abortion rates of the figs were monitored, and the remaining ripe figs were harvested and their contents were recorded. The features of measuring are pollinator progeny, male and female flowers and bladders (unoccupied, empty but galled female flowers).

Results

There were fifty percent of harvest figs in the pollen carrying or control experiment (30/60) whereas in the pollen-free or treatment experiment was twenty percent (12/60) left. Means ±SD of exit galls was 56.27 ±14.99 in control and 27.75 ±16.31 in treatment. The bladder number in the control was 30.47 ±15.33 while in the treatment was 52.50 ±23.16 (Table 5.2, 5.3).

Duration of fig development was diverse from 30 days to 71 days, however both experiments took average 41 to 46 days for reproductive stage. In pollen carrying experiments, the abortion figs commonly represented in two weeks after pollinated, whereas it took longer (2-4 weeks) in pollen free carrying experiment (Table 5.2, 5.3).

The exit galls were the galls contained progeny pollinators that divided to male and female wasps. In pollen-free experiment, the ratio of male and female was 5.92: 21.83 (Table 5.2) or about 1:4, whereas in control was 8.70: 47.90 (Table 5.3) or about 1:5.5.

Abortions occurred in figs entered by both pollen carrying and pollen-free foundresses, but were significantly more frequent in figs that had not been pollinated ($\chi 2 = 11.87$, $P<0.01$, $df = 1$; Figure 5.3, Table 5.4). The figs that survived through to maturity (treatment No. 9) included one that produced no fig wasps, but contained numerous bladders. Normally, abortion figs had bright yellow color and fig turned soft.

Table 5.2 The feature components of *F. montana* in pollen-free experiment (treatment)

No.	exited gall	bladders	unpollinated flowers	total flowers	male flowers	male wasp	female wasp	duration (days)
1	17	52	9	78	18	2	15	46
2	37	37	8	82	15	4	33	39
3	45	19	43	107	17	10	35	46
4	53	37	28	118	13	5	48	46
5	18	62	3	83	15	1	17	44
6	52	62	2	116	7	4	48	43
7	23	71	0	94	16	2	21	43
8	22	29	30	81	11	4	18	42
9	0	94	4	98	16	0	0	44
10	13	53	18	84	11	6	7	40
11	21	84	7	112	17	2	19	40
12	32	30	5	67	12	31	1	30
Sum	333	630	157	1120	168	71	262	503
Mean	27.75	52.50	13.08	172.31	14.00	5.92	21.83	41.92
SD	16.31	23.16	13.66	285.19	3.25	8.33	16.21	4.46

Table 5.3 The feature components of *F. montana* figs in pollen-free experiment (control)

No.	exited gall	bladders	unpollinated flower	total flowers	male flowers	male wasp	female wasp	duration (days)
1	50	22	0	74	12	8	42	52
2	71	37	6	114	16	5	66	71
3	69	45	5	119	14	8	61	52
4	63	27	4	94	10	19	54	69
5	64	24	1	99	27	5	59	54
6	60	15	12	87	14	10	50	63
7	58	28	5	91	12	8	50	52
8	62	29	24	115	16	10	52	53
9	65	30	12	107	14	11	54	52
10	52	42	4	98	10	10	42	51
11	64	40	8	112	12	12	52	42
12	52	43	7	102	20	6	46	45
13	73	11	2	86	12	6	67	43
14	60	21	7	88	17	7	53	42
15	14	68	3	85	17	1	13	44
16	79	4	9	92	14	3	76	41
17	45	58	0	103	21	8	37	40
18	27	26	27	80	9	3	24	41
19	62	36	0	98	16	4	58	44
20	59	34	5	98	11	3	56	41
21	53	39	4	96	16	8	45	40
22	41	43	5	89	10	7	34	40
23	34	56	0	90	12	9	25	40
24	57	34	22	113	19	3	54	44
25	88	6	16	110	15	55	33	40
26	68	19	6	93	16	13	55	36
27	45	33	12	90	17	4	41	36
28	45	19	0	64	16	6	39	39
29	52	11	5	68	10	7	45	39

Table 5.3 The feature components of *F. montana* figs in pollen-free experiment (control) (continued)

No.	exited gall	bladders	unpollinated flower	total flowers	male flowers	male wasp	female wasp	duration (days)
30	56	14	4	74	20	2	54	39
Sum	1688	914	217	2829	445	261	1437	1385
Mean	56.27	30.47	7.23	94.30	14.88	8.70	47.90	46.17
SD	14.99	15.33	7.08	13.98	4.00	9.52	13.49	9.06

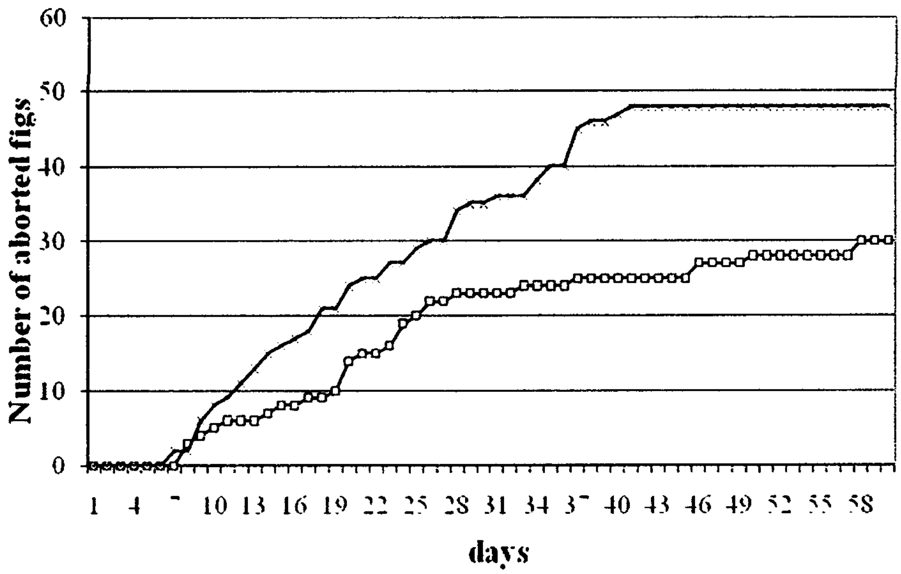
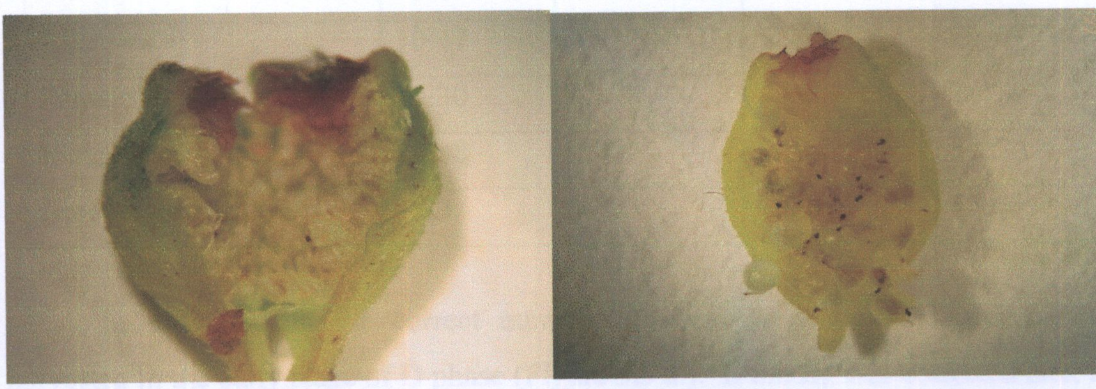


Figure 5.3 The cumulative numbers of *Ficus montana* male figs aborting after entry by single pollen-free (x–line, n = 60) or pollen-carrying foundresses (□ –line, n = 60).

Table 5.4 chi-square test of abortion *F. montana* figs in pollen free experiment.

observed values	abortion	harvest	Total
control	30	30	60
treatment	48	12	60
total	78	42	120
expected vales			
	39.00	21.00	
	39.00	21.00	
P value	0.00	df	1
Chi value	11.87		

Abortion figs that failed in a couple weeks after pollination contain mostly non pollinated flowers. There were small flowers packed in small fig (Figure 5.4 a.). The abortion figs which failed after two weeks of pollination were large with galling size containing some developed flowers (Figure 5.4 b.). However, in this case the wasp larvae always died before reaching to develop successfully that the gall flowers were called 'bladders'. The color of bladders was represented in both white and brown galls with brown stigma.



a. b.

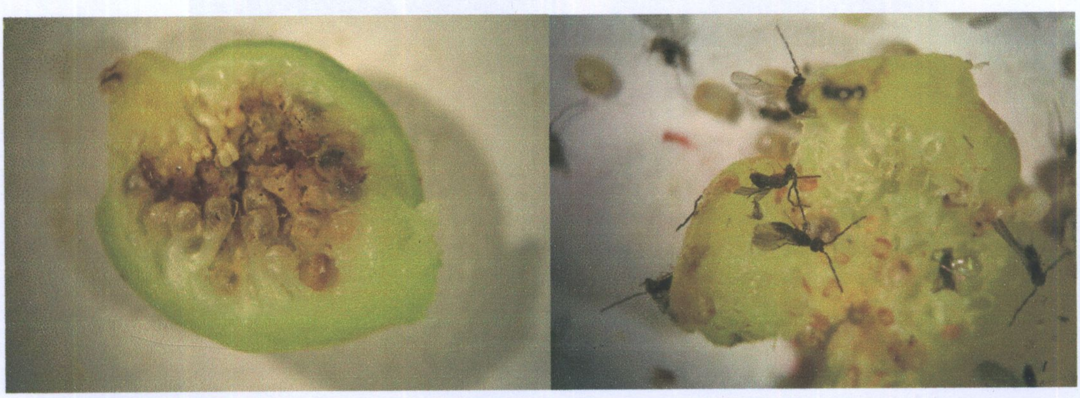
Figure 5.4 The dissection of abortion *F. montana* figs; *a.* The fig failed within two weeks after female wasp entering, and *b.* The fig failed during three or four weeks after entering.

Overall, the figs entered by pollen-carrying wasps that reached maturity produced over twice as many pollinator progeny as those that did not (Table 5.4, Z test, z (30, 12) = 5.27, ρ <0.001). The sex ratios amongst the progeny did not differ significantly (Z test, z (30, 12) = 0.932, ρ > 0.05). This difference in the numbers of progeny produced was reflected in the presence of far more bladders in those figs that lacked pollen. The numbers of undeveloped flowers were similar in the two groups of figs, suggesting that foundress activity had been unaffected (Table 5.5).

Table 5.5 The contents of *F. montana* figs that completed their development following the introduction of a single pollen-carrying or pollen-free foundress.

Contents	Pollinated (N=30)		Without pollen (N=12)	
	Mean	SD	Mean	SD
Pollinator progeny	56.60	15.26	27.75	16.31
Male progeny	8.70	9.52	5.92	8.33
Female progeny	47.90	13.49	21.83	16.21
% male progeny	15.37	-	21.33	-
Seeds	0	0	0	0
Bladders	30.47	15.33	52.50	23.16
Female flowers	94.30	13.98	93.50	16.58
Male flowers	14.88	4.00	14.00	3.25
Non pollinated flowers	7.23	7.08	13.08	13.66

In order to get the correct number of wasp progeny ratios, the fig was harvested in the early stage of D phase (Figure 5.5 a.). If the fig was collected late, the female pollinators would emerge when the ostiole became looser (Figure 5.5 b.). Hence, at that time, male and female galls would not be distinguishable. In this study, the former emerging wasp was male. After emerge, they walked around in the fig and mated the female from outside their galls. One male wasp could mate with more than one female.



a. b.

Figure 5.5 Dissection of male fig; a. early maturity phase (D-phase), b. female pollinators emerge

In the experiment of pollen-free carrying, information that received was the male fig that immerged with non-pollen foundress could not produce any seeds. It was shown that female flowers in male fig (gall) of *F. montana* could not develop themselves to be fruits and seeds without pollination (Table 5.5).

5.1.5 Experiment II

Oviposition prevention

Male figs of *F. montana* were bagged at the pre-receptive stage as before. Foundresses were allowed to emerge naturally from figs that had been collected the day previously and placed in vials covered with fine mesh. The wasps were then cooled briefly in a freezer before half were placed above an ice-chamber and had the tips of their ovipositors cut transversely with a scalpel. The wasps were then left for about 30 minutes to recover at room temperature and their longevity appeared unaffected by the treatment. Twenty control and 20 maimed foundresses were then introduced singly, as before, into the previously bagged figs, and the bags were replaced. The fine bags were removed in a week later (Figure 5.6a.). The treatment and control figs were located on the same plants. The figs were monitored similar to the experiment I and their contents at maturity recorded (Figure 5.6b.).

a. b.

Figure 5.6 Fig with oviposition experiment; *a.* control experiment that fig was pollinated and oviposition, *b.* dissected fig for measuring.

Results

Foundresses with cut ovipositors showed typical behavior at the ostioles, readily entering the figs. All of the 20 figs entered by these foundresses had aborted after three weeks (Figure 5.7) and when the figs were opened they were found to contain only undeveloped male and female flowers (Figure 5.8).

Most figs without oviposition failed in a few weeks. Some of them could survive longer but they turned abort. The longer survival figs showed the develop galls inside, it seemed to be gall flowers developed when they received the pollen. However, no fig reached maturity. The result showed that the male fig of *F. montana* could not produce seeds without oviposition.

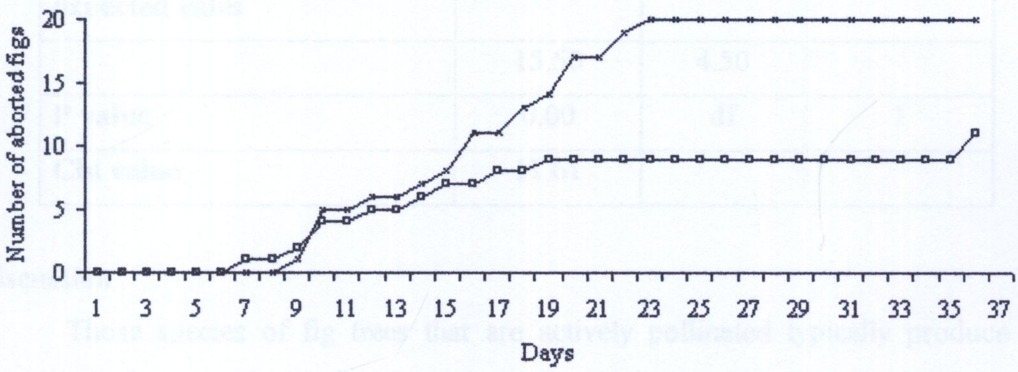


Figure 5.7 Cumulative abortions amongst *Ficus montana* male figs after entry by single foundresses with (□–line, n = 20) and without intact ovipositors (x–line, n = 20).

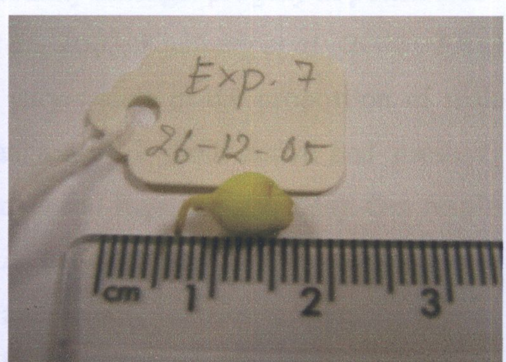


Figure 5.8 Fig without oviposition; *a.* the falling figs in 7-10 days (ovipositor removed), *b.* falling fig after 10 days.

The falling figs within 7-10 days after the wasp entered showed that female flowers did not develop to gall. Meanwhile, the longer survival figs showed galled inside.

Eleven of the control figs also aborted, but the rate of abortion was significantly lower in these figs ($\chi 2 = 11.61$, $P<0.01$, $df= 1$) (Table 5.6).

Table 5.6 The chi-square test of abortion figs in the prevented oviposition experiment.

observed values	**abortion**	**harvest**	**total**
control	11	9	20
treatment	20	0	20
total	31	9	40
expected vales			
	15.50	4.50	
P value	0.00	df	1
Chi value	11.61		

Discussion

Those species of fig trees that are actively pollinated typically produce far fewer male flowers than those species that rely on passive pollination (Kjellberg *et al.*, 2005). This improvement in efficiency has clear benefits for the plant, as it can direct resources and more of the limited space within the fig to the production of additional female flowers, but the benefits of active pollination for the pollinators have been less clear. Some studies have detected increased mortality amongst progeny in pollen-free figs, others have not (Nefdt, 1989; Jousselin *et al.*, 2003; Kjellberg *et al.*, 2005). *Ficus montana* is unusual in that individual plants vary widely in the proportion of male flowers present in their figs, covering the range seen in both active and passively pollinated species (Kjellberg *et al.*, 2005; Suleman and Raja, unpublished). Our results show that there are strong sanctions against *L. tentacularis* foundresses that fail to collect pollen, at least in those figs where they are the only females to enter.

Pollen-free figs were more likely to abort, and when they did not abort, far fewer progeny were produced. The associated increase in the numbers of bladders suggested that flowers were being galled, but a smaller proportion of their larvae survived. Whereas pollination has a significant impact on fig wasp reproductive success, it may not be the main stimulus responsible for the retention of male figs by the plant, as all the figs where oviposition was prevented aborted within three weeks. The act of oviposition (or gall production) may, therefore, be essential for figs to be retained, with pollination increasing the likelihood that retention occurs. It must be borne in mind, however, that relatively little pollen may have been dispersed by the maimed wasps, even though they appeared to be as vigorous as control females. This is because it is normally dispersed at about the same time as oviposition. Repetition of this experiment using a passively pollinating fig wasp and its host plant would be valuable, and if confirmed, then male fig development contrasts with the situation in female figs, where no oviposition and galling take place and pollination must be the stimulus for floral development to continue. Seeds have never been detected in any male figs of *F. ontana*, strongly suggesting that female flowers in male figs are physiologically incapable of producing seeds, even if they do receive pollen.

5.2 MONOECIOUS FIG

The pollination study of *Ficus racemosa* L.

5.2.1 Introduction

The interaction between *Ficus* and their pollinators is an important model for studying obligatory mutualism. Between monoecious and dioecious figs the mechanisms are different. Monoecious figs contain three kinds of flowers in the same fig and same tree, whereas dioecious female and male trees were separated (Kjellberg *et al.*, 2001).

F. racemosa is a member of subgenus *Sycomorus*, which is one of a few monoecious species in this group (Berg, 1989). Its distribution range is from India to Australia (Corner, 1965). In Thailand, it was found in all part of the country, especially in moist areas and along rivers (Gardner *et al.*, 2000). The fig tree is a large tree that can reach up to 30 m high with a great number of cauliflorous syconia bearing and producing a large number of figs in each crop year-round (Wang *et al.*, 2005). Inside a syconium, there are three kinds of flowers: male, female and gall flowers. The large number of tiny flowers with those flowers packed on the inner surface (Wiebes, 1979). Female flowers in monoecious figs produce both seeds and wasp offspring at the same time. The flowers with short style (gall flower) produce insects, while the type of long style flowers produce seeds (Berg and Wiebes, 1992). The proportion of flowers inside the fig is various in different species, therefore the trade off between them and this system sustaining is the interesting point to study (Wang *et al.*, 2005).

Many publication reported that people used their fruits and leave as vegetable. The leave can be used for vegetable and medicinal plant. Mandal *et al.* (2000) studied an anti-inflammatory property of *F. racemosa* leaf extract and reported that 200 and 400 mg/kg extracts was found to possess significant anti-flammatory activity. Khan and Sultana (2005) found that the powder extract from this fig species can also be a potent chemopreventive agent and suppresses Fe-NTA-induced renal carcinogenesis and oxidative damage response in Wistar rats. Rahuman *et al.* (2008) reported the extracts of leaf and bark of *F. racemosa* can against the early fourth-instar larvae of *Culex quinquefasciatus* (Diptera: Culicidae).

5.2.2 Literature review

The pollination process starts with the pollen-carried female wasps emerged from the natal fig then looked for the new receptive fig for laying eggs. In dioecious figs, she is able to succeed in laying eggs only in male fig and produce seed in female figs. While she can success in both laying eggs and pollination in the same syconium of monoecious figs (Kjellberg *et al.*, 2005). Hence, inside the monoecious fig, the female flowers are shared for seeds and wasps production. The factors affecting the system maintenance of their production were very interesting for investigation (Corlett, *et al.*, 1990).

F. racemosa is pollinated by specific obligated wasp, *Ceratosolen fusciceps* Mayr (Berg and Wiebes, 1992). Its fig is 3-5 cm in diameter when mature with pear shape. The color of fig is green or purplish green in the early stage then turn to reddish orange when mature.

This fig species has an active pollination mode, which means pollinators need to have specialized structure that called "pollen pocket" to collect pollen. Before leaving their natal fig, female pollinators will pick some pollen with their forelegs and introduce it into pollen pocket. The behavior was the activity of pollination and oviposition which was done at the same time (Kjellberg *et al.*, 2001).

At receptive phase, inside monoecious fig flowers were packed in several layers but the entire stigmas placed in the same height (Ganeshaiah and Kathuria, 1999). As well as other monoecious, *F. racemosa* has a large number of female flowers densely packed inside syconium. The stigma arranged in the same layer continuously (Berg and Wiebes, 1992). The female pollinator went into the fig cavity then started pollinating and ovipositing by walking around on the layer of stigma. Afterwards, seeds and wasp larvae develop inside female flowers and the fig cavity was filled with liquid until the maturity. It was normally found in *Sycomorus* and may be the function of larva and pollinative protection (Berg and Corner, 2005).

The periods of flowering and fruiting are also various in each fig species. Wang *et al.* (2005) reported that the period of flowering to fruiting of *F. racemosa* needed no more than 2 months in the rainy season and 2 or 3 months in dry season to complete. It showed that the season and climate are important effects their growth and development periods. Several monoecious figs were studied and the periods of development were devided to six phases (Table 5.7).

In the wild, *F. racemosa* fruits are food for squirrels, monkey, fruit-eating bats, and birds. Particularly, during fruit ripening, insects are also beneficial to insectivorous birds.

Normally, these trees grow along river blanks and function to be an erosion protective plant. In Chiang Mai, *F. racemosa* is widely distributed everywhere both the wild and urban areas. Hence, a study of *F. racemosa* pollination would not only serve the knowledge of plant and insect co-evolution, but also support the future studies such as the benefit, germination, dispersal of this plant.

5.2.3 Materials and methods

Studied species

***Ficus racemosa* L.** (Figure 5.9)

Trees, 25-30 m tall, monoecious; bark grayish brown, smooth; branchlets, stipules ovate-lanceolate, 1.5-2 cm. **Leaf**: ovate-lanceolate, 5-8 x 10-15 cm, glabrous; base cuneate; margin entire; apex acute; young leaf blades and figs with bent hairs. Petiole 2-6 cm. **Figs**: paired or cluster on leafy branchlets, reddish orange when mature, pear-shaped, 2-5 cm in diam., basally attenuate into a stalk; peduncle ca. 1 cm; involucral bracts triangular-ovate. Male, gall, and female flowers within same fig. **Male flowers**: near apical pore, sessile; calyx lobes 3 or 4, spatulate; stamens 2. **Gall flower**: both short and long pedicel present; calyx lobes broadly with 3- or 4-toothed; style lateral. **Female flowers**: short pedicel; calyx lobes broadly, apex 3- or 4-toothed; style lateral and long; stigma clavate. **Fruit**: achene, subglobse. **Flowering** and **Fruiting**: year-round.

Table 5.7 Six phases of fig development in monoecious fig species (Galil and Eisikowitch, 1968; Wiebes, 1979; Yang *et al.*, 2002).

Fig development	**Characters**
Phase A or prefloral	The initiation of fruiting occurrence
Phase B or female phase	The female flowers mature several weeks before male flowers. It becomes "receptive" and the figs release some species-specific olfactory compounds which attract the pollinator wasp. The female flowers in the monoecious figs show a variation in style lengths. Wasps must oviposit in the ovaries of flowers having styles shorter than their ovipositor. The flowers with styles longer than the ovipositor are not oviposited into and if pollinated these flowers bear seeds.
Phase C	The wasp larvae develop in the flowers where eggs were laid while the rest of pollinated female flowers develop into seeds. The unpollinated flowers remain vacant while some flowers develop into bladders, which are flowers that appear galled, but contain unsuccessful developed larvae.
Phase D or male phase	The next generation of wasps emerge. The male wasps come out first and chew to open the ovaries containing female wasps after mating. Male wasps then make the hole through out for female leaving and they usually die at the natal fig. At this time, the male flowers in the fig dehisce and release pollen. The female wasps emerge and often shovel pollen from the anthers into their meso-thoraic pollen pockets. These female wasps then leave the natal fig through the tunnel dug by the male and fly out in search of other receptive figs.
Phase E or post floral phase	The wasps leave the fig. It swells and ripens and is dispersed by animals such as fruit eating mammals and birds.
The emergent wasp phase	The newly emerged adult female wasps look for the receptive fig in the other plants to lay her eggs and also pollinate. The lifespan of them depend on species. Normally wasps cannot survive more than two or three days.

a. b.

Figure 5.9 Studied species; *Ficus racemosa* L., *a.* tree, *b.* figs on the branches

Field observation

Phenological censuses of *F. racemosa* were made in urban areas of Chiang Mai at elevation from 313-372 m above sea level (Table 5.8). Five fig trees were monitored during September 2006-September 2007. The census was made each crop of all the sampling tree as follows;

1. Fig bearing; count the number of figs in the early D-phase in each crop
2. Leaf duration; check the periods of bearing and falling leaves.
3. Style length measuring in the B-C phase; collect 10 figs from 5 trees in the rainy and the dry season to study in the laboratory.
4. Observe behavior of pollinators during fig development and record; the number of foundress, the behavior of male and female pollinators, the sequence of wasps emerging, etc.

Table 5.8 The locations of the studied fig *F. racemosa* in urban areas of Chiang Mai.

No.	Sampling tree	Altitude (m asl.)	Latitude	Longitude
1	T1	329.4	18° 47′ 97.3" N	98° 57′ 16.3" E
2	T2	368	17° 48′ 13.1" N	98° 57′ 04.7" E
3	T3	335.5	17° 48′ 26.6" N	98° 57′ 23.7" E
4	T4	371.3	17° 47′ 68.7" N	98° 56′ 79.7" E
5	T5	313.8	17° 48′ 64.9" N	98° 58′ 74.0" E

Laboratory study

1. Plant specimens, such as leaves, shoots, and syconia were taken to the laboratory for morphological fig wasps studying.
2. Style measuring; figs in the B-C phase were collected to dissect with longitudinally from ostiole to pedicel. Fifty sampling female flowers in the each fig of 5 fig trees were measured under a stereomicroscope.
3. Twenty figs in early D phase were collected and kept in small containers that covered by fine cloth. All of wasps emerged were then dried for counting. The figs were taken to dissect in search of some remaining wasps and to sample their seed production.
4. Wasps were identified inside the syconia and the number of male, female pollinators, non pollinators and seeds were counted.
5. Both plant and insect specimens were preserved in 70 % alcohol solution for future study.
6. Morphological characters of the figs and their pollinators were described by description and they were photographed.

Data analysis

T-test was used to analyze quantitative measurements such as number of figs/tree, seeds/fig, male, female and total wasps/figs, etc.

The hypothesis was "Is it different in the number of seed and wasp production between dry and rainy seasons?"

Climate data (2006-2007)

The dry season in Chiang Mai is composed of dry and cold (winter) and dry and hot (summer) periods. The average temperature was about 21-22 ° C during November and January. The relative humidity was between 70-77 % RH (Figures 5.10 and 5.11). In summer, during March and mid of May, the average temperature was 26-29 ° C and the relative humidity was between 51-67 % RH (Figures 5.10 and 5.11). The rainfall was highest in May at 400 mm and the annual rainfall was 1,251.9 mm (Figure 5.12).

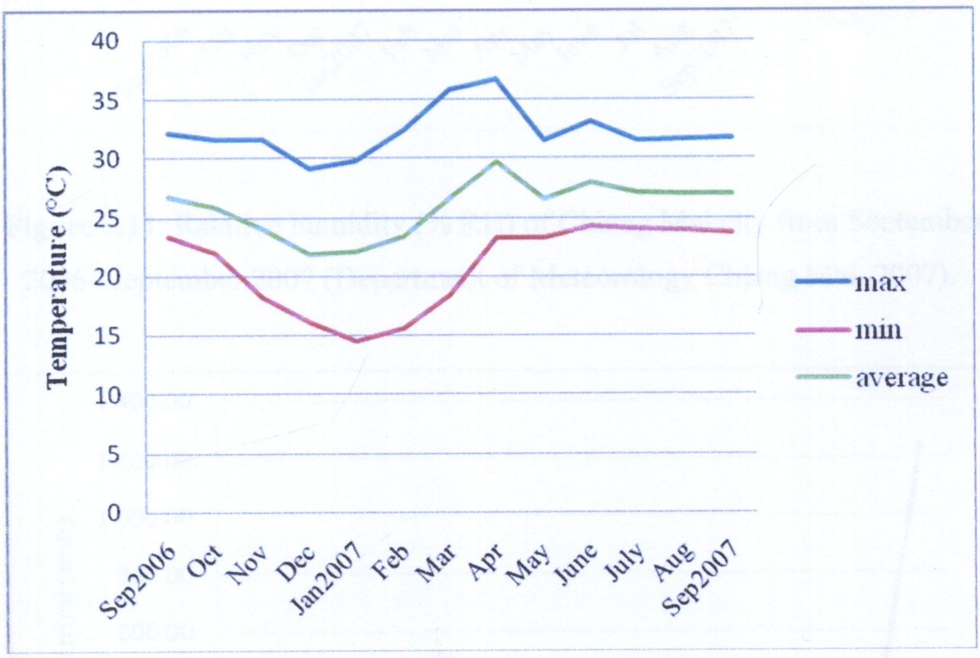


Figure 5.10 Temperature (C°) of Chiang Mai city from September 2006-September 2007 (Department of Meteorology, Chiang Mai, 2007).

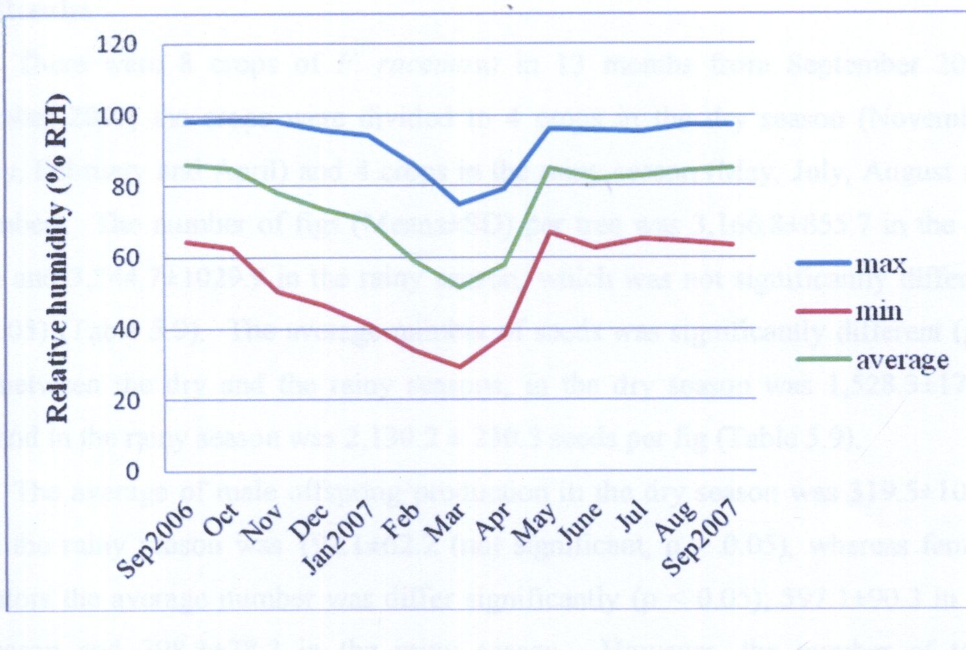


Figure 5.11 Relative humidity (% RH) of Chiang Mai city from September 2006- September 2007 (Department of Meteorology Chiang Mai, 2007).

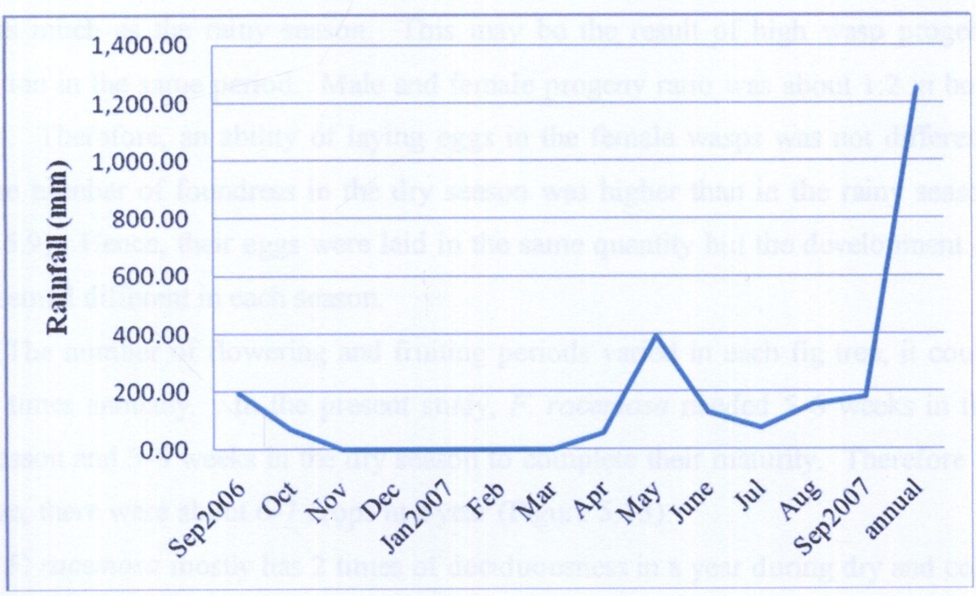


Figure 5.12 Rainfall (mm) of Chiang Mai city from September 2006-September 2007 (Department of Meteorology, Chiang Mai, 2007).

5.2.4 Results

There were 8 crops of *F. racemosa* in 13 months from September 2006-September 2007, the crops were divided to 4 crops in the dry season (November, January, February and April) and 4 crops in the rainy season (May, July, August and September). The number of figs (Means±SD) per tree was 3,166.8±855.7 in the dry season and 3,544.7±1029.9 in the rainy season, which was not significantly different ($\rho > 0.05$) (Table 5.9). The average number of seeds was significantly different ($\rho < 0.05$) between the dry and the rainy seasons; in the dry season was 1,528.3±171.6 seeds and in the rainy season was 2,130.2 ± 230.3 seeds per fig (Table 5.9).

The average of male offspring production in the dry season was 319.5±100.1 and in the rainy season was 192.1±62.2 (not significant, $\rho > 0.05$), whereas female pollinators the average number was differ significantly ($\rho < 0.05$); 597.1±90.3 in the dry season and 398.3±78.2 in the rainy season. However, the number of total pollinators was not significant ($\rho > 0.05$); 835.5±297 in dry season and 671.5±110.9 in rainy season (Table 5.9).

The number in female progeny increased in the dry season, which was about twice as much as the rainy season. This may be the result of high wasp progeny production in the same period. Male and female progeny ratio was about 1:2 in both seasons. Therefore, an ability of laying eggs in the female wasps was not different, even the number of foundress in the dry season was higher than in the rainy season (Table 5.9). Hence, their eggs were laid in the same quantity but the development of larva seemed different in each season.

The number of flowering and fruiting periods varied in each fig tree, it could be 7-8 times annually. In the present study, *F. racemosa* needed 5-6 weeks in the rainy season and 5-8 weeks in the dry season to complete their maturity. Therefore in each tree, there were about 6-7 crops in a year (Figure 5.13).

F. racemosa mostly has 2 times of deciduousness in a year during dry and cold season (January-February) and rainy season (August-September).

Table 5.9 The number of figs, seeds and pollinator wasps in the dry and rainy seasons between September 2006 and September 2007 in Chiang Mai city.

Number	Season	Number of Trees	Cropping time	Mean	SD	ρ-value	Significance
Figs	Dry	5	4	3,166.8	855.7	0.546	NS
	Rain	5	4	3,544.7	1029.9		
Seeds	Dry	5	4	1,528.3	171.6	0.002	S
	Rain	5	4	2,103.2	230.3		
Male wasps	Dry	5	4	319.5	100.1	0.074	NS
	Rain	5	4	192.1	62.2		
Female wasps	Dry	5	4	597.1	90.3	0.016	S
	Rain	5	4	398.3	78.2		
Total wasps	Dry	5	4	835.5	297	0.341	NS
	Rain	5	4	671.5	110.9		
Foundress	Dry	5	4	11	7.1	0.015	S
	Rain	5	4	6.2	4.3		

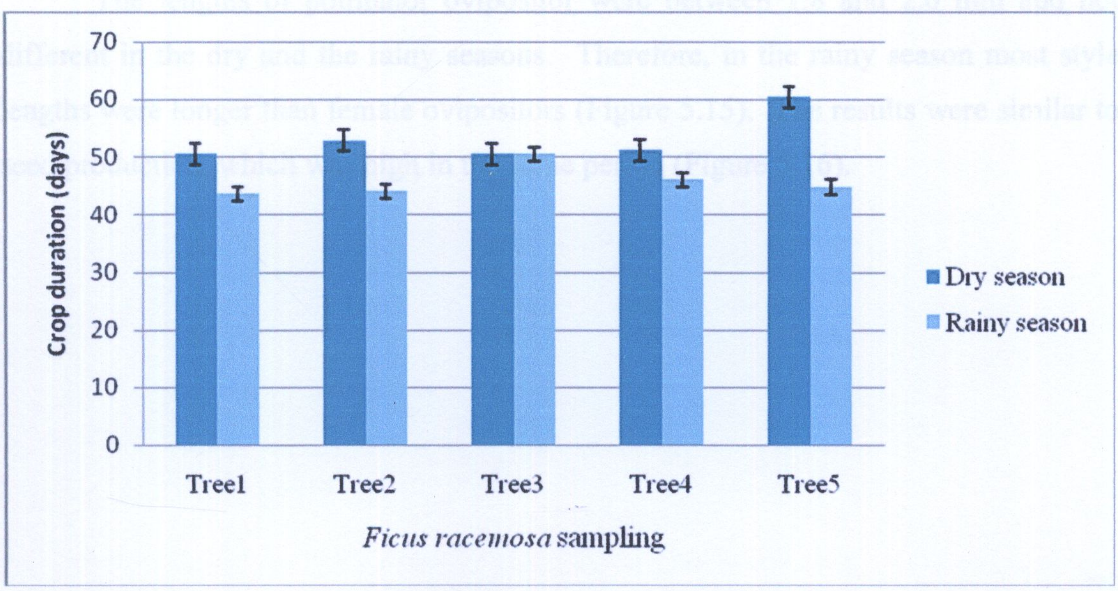


Figure 5.13 Crop duration of 5 fig trees, *F. racemosa* between the dry and the rainy season.

One of the factors that believed to be an important reason for different ratio of seeds and progeny production was "style length". In *F. racemosa*, there are various style lengths in female flowers. Female flowers in monoecious figs can produce both seeds and wasp offspring. Hence, the style length in different crops between the dry season, and the rainy season were observed and measured (Figures 5.14 and 5.15).

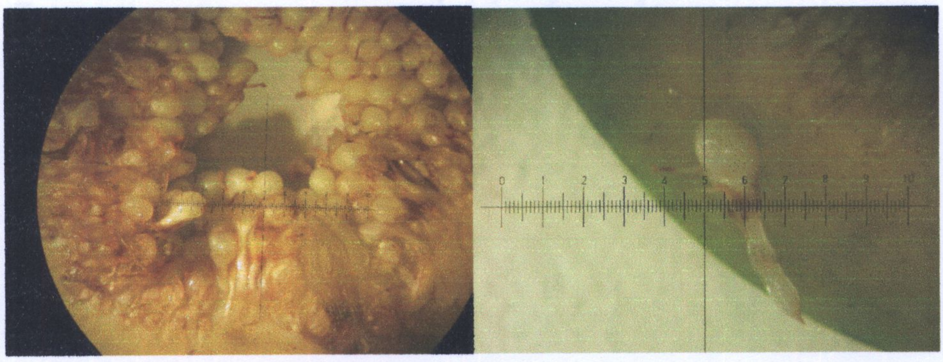


Figure 5.14 Style lengths measuring of a female flower fig

In the rainy season, the average lengths of style (50 style sampling/fig) in most of the studied figs was between 1.73 and 2.16 mm, whereas in the dry season it was between 1.70 and 1.95 (Figure 5.15). The means of style length in different seasons revealed the opposite way as the number of seeds and female wasp production.

The lengths of pollinator ovipositor were between 1.8 and 2.0 mm and not different in the dry and the rainy seasons. Therefore, in the rainy season most style lengths were longer than female ovipositors (Figure 5.15). The results were similar to seed production, which was high in the same period (Figure 5.16).

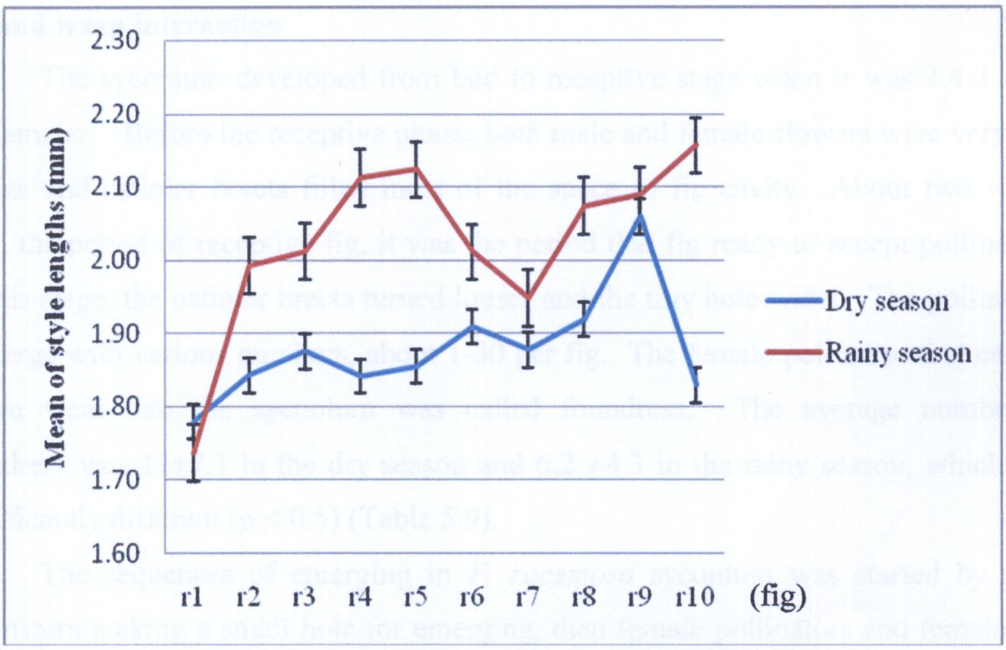


Figure 5.15 Mean of style length (mm) in the dry and the rainy seasons, r1-r10 were the average of style lengths sampling in each fig.

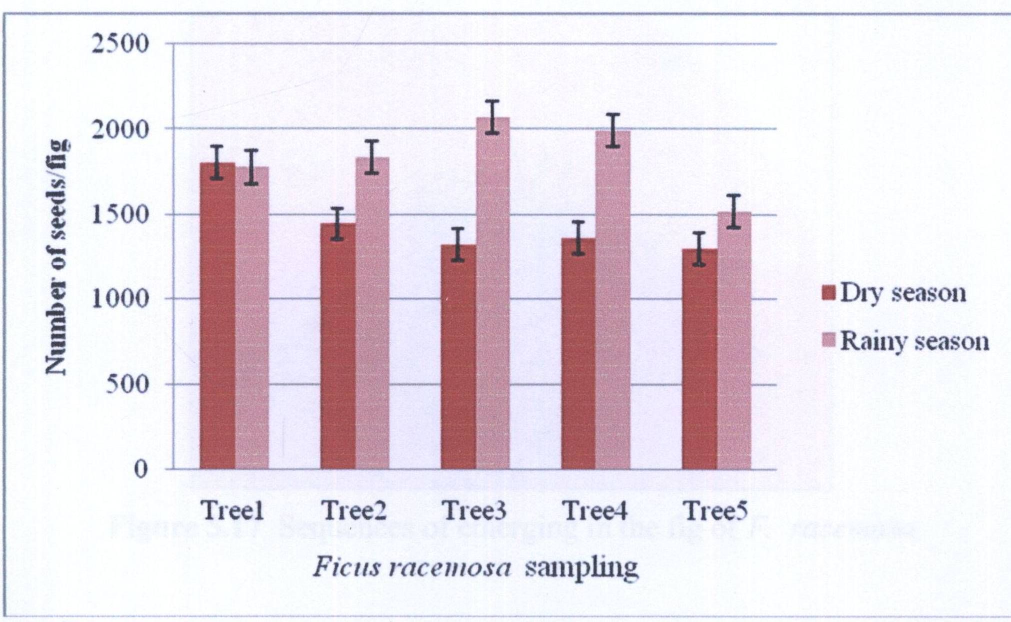


Figure 5.16 The number of seeds fig in each sample tree, *F. racemosa*

Fig and wasp interaction

The syconium developed from bud to receptive stage when it was 2.4-3.2 cm in diameter. Before the receptive phase, both male and female flowers were very tiny in size and ostiolar bracts filled most of the space of fig cavity. About two weeks later, the period of receptive fig, it was the period that fig ready to accept pollinators. At this stage, the ostiolar bracts turned looser and the tiny hole wider. The pollinators immerge with various numbers, about 1-30 per fig. The female pollinator that carried pollen went into the syconium was called foundress. The average number of foundress was 11±7.1 in the dry season and 6.2 ±4.3 in the rainy season, which was significantly different ($\rho < 0.5$) (Table 5.9).

The sequences of emerging in *F. racemosa* syconium was started by male pollinators making a small hole for emerging, then female pollinators and female non pollinators both come out almost at the same time (Figure 5.17). Early period of emerging, most male pollinators first appeared at the tiny hole of receptacle. Some figs, two or three holes were made, and the prior emerged group was also male pollinator wasps.

Figure 5.17 Sequences of emerging in the fig of *F. racemosa*

Not only female pollinators used the benefit of fig trees, but also female non pollinators. They could lay their eggs from the outside of the syconium (Figure 5.18), sometimes made galls and sometimes function as parasitoid.

The dominant character of female non pollinator was the long ovipositor that essential for eggs laying. The number of non pollinators was also tendency to the production of pollinators.

Five species of non pollinator wasps were found which consisted of two species of *Apocrypta* and three species of *Platyneura (Apocryptophagus)*. Number of non pollinator production was also high in dry season and the dominant species were *P. testacea* and *P. mayri* (Figure 5.19). The highest number of *P. testacea* per fig was 34.6 in November (Figure 5.19). The male of non pollinators emerged together with male pollinators inside fig, but their size was very small and difficult to classify.

Figure 5.18 Oviposition of *Apocrypta* sp. from out side the fig, and gall making by the female non pollinators.

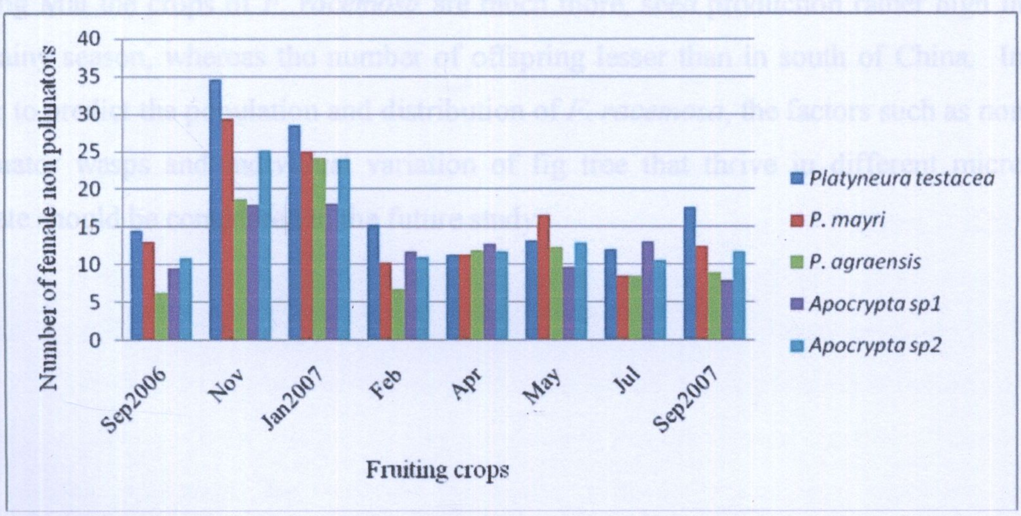


Figure 5.19 Number of female non-pollinator offspring in each crop from September 2006-September 2007.

The active period of female pollinator wasps was about 2-3 hours after emerging when they were left in the small container at room temperature. Next two or three hours, they could survive, but had less activity. On the other hand, non pollinators could leave longer, it took more than 24 hours at the same condition.

5.2.5 Discussion

The periods of fig maturity were lesser than the same species in Southern China which it took more than 2 months (8 weeks) in the rainy season and 2 or 3 months (8 or 12 weeks) in the dry season (Wang *et al.*, 2005). And also the number of seeds and offspring were lesser than the previous study in China.

Its non pollinators are three species of *Apocryptophagus* (Sycophaginae) and two species of *Apocrypta* (Sycoryctinae). The former genus is a competitor with pollinators, while the latter is a parasite of other wasps. (Kerdelhue *et al.*, 2000 and Weiblen, 2002). The community of non pollinators has more or less impact on fig and pollinator interaction, however the information of non pollinators fig wasp is poorly known (Kjellberg *et al.*, 2005).

Wang *et al.* (2005) compared the proportion of seeds and gall flowers in each fruit of *F. racemosa* between the rainy (May to October) and the dry season (November to following May) in south of China, it was showed that gall production in the dry season (January and November) was higher than rainy season, whereas seeds production was rather stable. This study showed the results in the same pattern but in Chiang Mai the crops of *F. racemosa* are much more, seed production rather high in the rainy season, whereas the number of offspring lesser than in south of China. In order to predict the population and distribution of *F. racemosa*, the factors such as non pollinator wasps and individual variation of fig tree that thrive in different micro climate should be considered in the future study.

CHAPTER VI

DISCUSSION AND CONCLUSION

6.1 TAXONOMIC STUDY OF SOME FIGS AND THEIR POLLINATORS

Twenty-Six fig species found in the ecological studies on figs from June 2005 to May 2007 in Chiang Mai, northern Thailand. They belonging to 6 subgenera. The largest subgenus, *Urostigma*, had 11 species, followed by *Sycomorus* with 8 species, *Ficus*, *Sycidium* and *Synoecia* each with 2 species and *Pharmacosycea* with 1 species. *F. benjamina* L., *F. hispida* L. and *F. racemosa* L. had 2 varieties each, but *F. fistulosa* Reinw. ex. Bl. had only 2 forms. *F. benjamina*, *F. hispida* and *F. racemosa* were common from 310-1,200 m asl., *F. anastomosans* (Corner) Berg and *F. anserina* Corner were adapted to limestone.

Fig wasps represented both pollinators and non pollinators. A large number of fig wasps were detected in every syconium, but only one species functioned as pollinator. Eight genera of pollinators found consisted of *Blastophaga, Ceratosolen, Dolichoris, Eupristina, Liporrhopalum, Odontofroggatia, Platyscapa and Pleistodontes.* Non pollinating fig wasps comprised of *Acophila, Apocrypta, Camarothorax, Ormyrus, Otitesella, Philotrypesis, Platyneura* (*Apocryptophagus*) and *Sycoscapter.*

The taxonomic revisions of figs in Thailand are on going. Then, in this study flora of the adjacent areas were used to discriminate species of figs.

Some characters are not clear to verify such as between female flowers of *F. auriculata* and *F. oligodon*, it is the same description in Flora of China. That character is very important to distinct female flowers in dioecious figs. Interestingly, it was reported that their pollinator was the same species, *C. emarginatus* Mayr (Wiebes, 1994), it would be possible to have the cross bred that promote some similar characters between them. However, this information has broken out the rule of one to one species. Although the variation in species is normally apparent, especially in different habitats and ecosystems, but if it is caused by pollination between species it can be different in morphology and lead to more difficulty in taxonomic work.

The knowledge about ecological aspects of the distribution are scattered in the literature and are often incomplete, and therefore not easy to summarize (Berg, 1989).

Sometimes, the complication caused by local names of the plants, e.g. fig tree, which is called 'Sai' in Thai is the one of sacred tree that the people avoid to cut down. Indeed many figs in *Urostigma* usually are also named 'Sai' such as *F. benjamina*, *F. macrocarpa*, *F. curtipes*, *F. maclellandii*. Another case is between *F. religiosa* 'Pho' and *F. rumphii* 'Pho khi nok'.

The widespread fig species usually possess a large number of individual species of pollinators. However, the number varied in each season. The figs with a small number of fig wasp populations were *F. ischnopoda* and *F. subincisa*. Many figs aborted in a few weeks. It may be as a result of the small population of the fig trees in the wild. The ripen fruits of *F. racemosa* are food many kinds of animals, so its seeds are expected to be dispersed widely. However, some fig species produce small-size fruits such as *F. benjamina*, but the large number of their figs attracted many kinds of bird, which help them dispersing seeds, as in *F. microcarpa* and *F. lacor*.

F. racemosa produced a large number of pollinators in each crop. It was different from the other monoecious figs both in fig size and number of seeds and wasps in the syconium. On the other hand, the figs with lesser number of fig wasp population were *F. anserina*, *F. subincisa* and *F. anastomosans*, many figs failed without entering. The cause may be the small population fig trees in the wild. Besides the pollinators, that effect to size of both populations, their dispersal carriers were also the important factor.

There were diverse types of fig tree characters represented such as leaf shape and syconium. However, within the species of dioecious figs, male and female figs always present the same characters in the wild. For the study of their morphology, it is difficult to separate the male from the female tree until their syconia occur.

In order to complete the knowledge of fig biology and classification, future studies on the details of interaction between figs and fig wasps should be of valuable work. It will support the knowledge of fig diversity, distribution and also conservation of natural ecosystems.

6.2 INTERACTION STUDY OF FIGS AND THEIR POLLINATORS

Interaction between figs and their pollinators is one of the popular subjects for biologists interested in co-evolution. Despite of more than 30 years of studies, the knowledge is still lacking due to their numerous species.

In the part of interaction of figs and pollinators, the Asian small shrub fig, *F. montana* Burm.f., was treated in the experiments. The question was about the benefit of fig and its pollinator, which is known as 'obligatory mutualism'. Both fig and wasp get their own benefits from the interaction, what happen if some activities fail?

The result showed that the non-pollinated figs could not succeed to maturity stage. Those figs turned yellow and failed before maturity, but female pollinators did the job of oviposition.

If none of pollinator entered, figs would fall within 7-10 days after receptivity stage. In the experiment of pollen-free, even more than half of them failed; some figs could succeed to ripe. The pollinators laid their eggs then the female flowers developed to be gall for serving their larva. It seemed that gall flower can develop by wasp oviposition, even though without pollination. It support the knowledge of 'chemical injection' that pollinator use for stimulate gall development (Kjellberg *et al.*, 2005). However, some larva grew, but the number of aborted fig increased. It seemed that the wasp could not get the benefit if pollination did not occur.

Therefore, gall flowers will develop completely by the action of wasp oviposition and pollination. This experiment showed that when fig did not receive pollen, its flower also did not develop perfectly. There were a high number of bladders and incomplete emerging pollinators. Some of early D-phase abortion fig showed that there was none of male wasp emerged from the gall and also none of female emerged. It supports the knowledge of female galls were penetrated and bitten by male wasp. It seems that the female cannot come out by herself without male wasp.

Inside the abortion fig, there are both brown and shiny white galls occurred. The brown galls, probably means bladders which is larva died inside but the white gall and shiny maybe the gall contained living larva or only recently death of larva. About 4 weeks after the fig developed, it was showed that male flower started to develop but never reached to pollen exposure.

The experiment of cutting ovipositor was carried out, in order to find the benefit of wasp oviposition activity to male fig. The result showed that all of figs rapidly fall after the receptive stage. It took about 2-3 weeks after foundresses entered. It was assumed that the female pollinators have taken the action of pollination because some gall flowers have developed and these figs lived longer than the fig without wasp entering. However, the developed gall of this experiment is smaller than the gall, in which eggs were laid. It might be selected to the knowledge of chemical injection, in this process it is only pollination but without lay egg, therefore, female wasps may not release some chemicals to induce gall and embryo development. It is believed that the embryo is a food supply of larva.

It was implied that plants gain benefits from pollinators to induce growth and development of embryo. In turn, if only pollination represent, wasp may not inject any chemical to stimulate the next step of flower development. Then, the syconium fail and no gall flowers became to produce seeds in *F. montana*.

In the observation study of *F. racemosa*, it was found that this fig tree needed only 5-6 weeks in rainy season and 5-8 weeks in dry season to complete their maturity. Therefore, about 6-7 crops occurred in a year. The periods were lesser than the studies on same species in Southern China, which it took more than 2 months (8 weeks) in rainy season and 2 or 3 months (8 or 12 weeks) in dry season (Wang *et al.*, 2005). And also the number of seeds and wasp offspring in this study were lesser that that in China.

The number of figs and male wasp production was not significantly different in the dry and the rainy season. On the other hand, the average number of seeds and female pollinators in the dry season were higher significantly than the rainy season. The results implied that fig trees produced the more suitable flowers for its reproductive in the rainy season and lesser in the dry season. It might be caused by the factors of seedling development, which might be better in the rainy season. On the other hand, in the dry season the number of seeds was increased while the number of offspring was higher than the rainy season. The same reason was the fig tree evolved to produce small number of seeds that will disperse in the dry season and may be less successful for development. Hence, the fig may produce the flowers that benefit for its pollinators instead. Its non pollinators were the three wasp species in *Platyneura* (*Apocryptophagus*) and two species in *Apocrypta*. The former genus was a competitor with pollinators, while the latter is a parasite of other wasps. (Kerdelhue *et al*, 2000 and Weiblen, 2002).

In the studies of interaction both monoecious and dioecious figs and their pollinators, it was implied that either fig trees or fig wasp pollinator have some adaptation to maintain their reproductive. It was not only the correlation between fig and pollinator but also relation to other factors such as climate and parasitic wasps. Hence, the results from this study can be used as baseline data to the study on figs. Future research would be considered on fig trees and fig wasp with other factors in ecology.

REFERENCES

Aigoin, D. and Kjellberg, F. 2006. *Les communautés de Micro-hyménoptères associés aux Ficus.* The Annual meeting of the Association for Tropical Biology and Conservation (ATBC), 18-21 July 2006, Kunming, Yunnan, China.

Banack, S.A., Horn, M.H. and Gawlika, A. 2002. Disperser- vs. establishment-limited distribution of a riparian fig tree (*Ficus insipid*) in a Costa Rican tropical rain forest. *Biotropica* 34 (2): 232-243.

Benders, H. E. 2002. *Strangler figs*. (Online), Available: http://blueplanetbiomes.org/ strangler figs.htm (17 May 2004).

Berg, C.C. 1989. Classification and distribution of *Ficus*. *Experientia* 45: 605-611.

Berg C.C and Wiebes, JT. 1992. *African fig trees and fig wasps.* Koninklijke Nderlandse Akademic van Wetenschappen Verhandelingen Afdeling Natuurkunde, Tweede Reeks, Deel 89: 1-298. Amsterdam.

Berg, C.C. 2003a. Flora Malesiana Precursor for the treatment of Moraceae 1: the main subdivision of *Ficus*. *Blumea* 48: 167-178.

Berg, C.C. 2003b. Flora Malesiana Precursor for the treatment of Moraceae 5: the subgenus *Sycidium*. *Blumea* 48: 573–579.

Berg, C.C. and Corner, E.J.H. 2005. *Flora Malesiana, series I, volume 17/part 2*: 1-70.

Berg, C.C. 2007. Precursory taxonomic studies on *Ficus* (Moraceae) for the Flora of Thailand. *Thai Forest Bulletin (Botany)* 35: 4-28.

Bouček, Z. 1988. *Australasian Chalcidoidea (Hymenoptera): A biosystematic revision of genera of fourteen families, with a reclassification of species.* UK: CAB international Wallingford.

Bronstein, J.L. 1988. Mutualism, antagonism and the fig pollinator interaction. *Ecology* 69: 1298-1302.

Bronstein, J.L. and McKey, D. 1989. The fig/pollinator mutualism: A model system for comparative biology. *Experientia* 45: 601-605.

Chantarasuwan, B. and Charernsuk, A. 2007. *Species diversity of Ficus* L. *(Moraceae) in Khao Nan National Park, Nakhon Sri Thammarat Province.* The 11th BRT Annual Conference, 15-18 October, 2007 Napalai, Udonthani. p 46.

Compton, S.G. and Hawkins, B.A. 1992. Determinant of species richness in southern Africa fig wasp assemblages. *Oecologia* 91:68-74.

Compton, S.G. and Nefdt, R.J.C. 1990. The figs and fig wasps of *Ficus burtt-davyi. Mitteilungen aus dem Institut fur Allgemeine Botanik in Hamburg* 23: 441-450.

Condit, J. 1969. *The exotic species.* USA: University of California: Division of Agriculture Science.

Cook, J. M. and Lopez-Vaamonde, C. 2001. Fig biology: Turning over new leaves. *Trend in Ecology & Evolution* 16 (1): 11-13.

Cook, J.M. and Rasplus, J.Y. 2003. Mutualists with attitude: coevolving fig wasps and figs. *Trends in Ecology and Evoltuion* 18: 241–248.

Cook, J.M., Bean, D., Power, S.A., and Dixon, D.J. 2004. Evolution of a complex coevolved trait: active pollination in a genus of fig wasps. *Journal of Evolutionary Biology* 17: 238–246.

Corlett, R.T., Boudville, V. and Seet, K. 1990. Seed and wasps production in five fig species (*Ficus*, Moraceae). *Malayan Nature Journal* 44: 97-102.

Corner, E.J.H. 1965. Check-list of *Ficus* in Asia and Australia with Keys to identification. *Gard. Bull. Singapore* 21: 1-186.

Department of Geography, Faculty of Social Sciences, Chiang Mai University. 2007. *Map of Northern Thailand.* (Online), Available: http:// www.geography. cmu.ac.th (07 October 2004).

Department of Meteorology Chiang Mai. 2007. Climatological data of Chiang Mai from 1971-2000. Report.

Endress, P.K. 1994. *Diversity and evolutionary biology of tropical flower.* Cambridge: Cambridge University Press.

Frank, S.A. 1989. Ecological and evolutionary dynamics of fig communities. *Experientia* 45: 674-680.

Galil, J. and Eisikowitch, D. 1968. On the pollination ecology of *Ficus sycomorus* in East Africa. *Ecology* 49(2): 259-269.

Ganeshaiah, K.N. and Kathuria, P. 1999. Does optimal packing of flowers in syconia shape style length in monoecious fig? *Biotropica* 31: 312-320.

Gardner, S., Sidisunthorn, P. and Anusarnsunthorn, V. 2000. *A field guide to forest trees of Northern Thailand.* Bangkok: Kobfai Publishing project.

Google map. 2007. *Map of Chiang Mai.* (Online), Available: http://www.googleearth.com. (06 July 2007).

Graham, M. and Round, P. 1994. *Thailand's Vanishing Flora and Fauna.* Bankok: Finance one public company Ltd.

Grison-Pige', L., Bessiere, J.-M., Turlings, C.J., Kjellberg, F., Roy, J. and Hossaert-Mckey, M. 2001. Limited intersex mimicry of floral odour in *Ficus carica. Functional Ecology* 15: 551-558.

Hampton, R.E. 1994. Introductory Biological statistics. USA: Wm.C. Brown Communications, Inc.

Harrison, R.D. 2005. Figs and the diversity of tropical rainforests. *BioScience* 55 (12): 1053-1064.

Herre, E.A. 1989. Coevolution of reproductive characteristics in 12 species of New World figs and their pollinator wasps. *Experientia* 45: 637-647.

Hooker, J.D. 1885. *Flora of British India Vol. V.* Kent: L. Reeve & Co., Ltd. 494-537.

Horn, M.H. 1997. Evidence for dispersal of fig seeds by the fruit-eating characid fish *Brycon guatamalensis* Regan in a Costa Rican tropical rain forest. *Oecologia* 109: 259-264.

Inthanon Research Station of Royal Project Foundation. 2007. *Climatological data of Inthanon Research Station of Royal Project Foundation from 2005-2007.* Report.

Jousselin, E. and Kjellberg, F. 2001. The functional implications of active and passive pollination in dioecious figs. *Ecol. Lett.* 4: 151-158.

Jousselin, E., Hossaert-Mckey, M., Herre, E.A. and Kjellberg, F. 2003. Why do fig wasps actively pollinate monoecious figs? *Oecologia* 134: 381-387.

Katharia-Gupta, P. 1999. *The pollination biology of monoecious fig tree in India.* PhD thesis (Biology), School of Biology, University of Leeds, UK.

Khan, N. and Sultana, S. 2005. Chemomodulatory effect of *Ficus racemosa* extract against chemically induced renal carcinogenesis and oxidative damage response in Wistar rats. *Life Sciences* 77: 1194–1210.

Kerdelhue', C. and Rasplus, J.Y. 1996. The evolution of dioecy among *Ficus* (Moraceae): an alternative hypothesis involving non-pollinating fig wasp pressure on the fig-pollinator mutualism. *Oikos* 77:163-166.

Kerdelhue', C. and Rasplus, J.Y. 1997. Active pollination of *Ficus sur* by two sympatric fig wasp species in West Africa. *Biotropica* 29: 69-75.

Kerdelhue C., Rossi J.P. and Rasplus J.Y. 2000. Comparative community ecology studies on old world figs and fig wasps. *Ecology* 81: 2832-2849.

Kjellberg, F. and Maurice, S. 1989. Seasonality in the reproductive phenology of *Ficus*: Its evolution and consequences. *Experientia* 45: 653-660.

Kjellberg, F., Jousselin, E., Bronstein, J., Patel, A., Yokoyama, J. and Rasplus, J.Y. 2001. *Pollination mode in fig wasps: the predictive power of correlated traits.* Proceedings of the Royal Society, London (B) 268: 1113-1121.

Kjellberg, F., E. Jousselin, M. Hossaert Mckey, and J.Y. Rasplus. 2005. Biology, ecology and evolution of fig-pollinating wasps (Chalcidoidea, Agaonidae). *In*: Raman, A., C.W. Schaefer and T.M. Wither (eds.) *Biology, Ecology, and Evolution of Gall-inducing Arthropods.* Science publishers, Inc: UK Plymouth. pp. 539-572.

Machado, C.A., Jousselin, E., Kejellberg, F., Compton, S.G.C., and Herre, E.A. 2001. *Phylogenetic relationships, historical biogeography and character evolution of fig-pollinating wasps.* Proceedings of the Royal Society, London (B) 268: 685-694.

Marduka, T. 2001. *Observation of birds and mammals visiting a fruiting fig at Niah National Park, Malaysia.* (Online), Available: http://www.mered.org.uk/Hornbill/Tan.htm (07 October 2004).

Michalound, G. 1988. *Aspect de la reproduction des Figuiers monoiques en Fôret Equatoriale Africaine.* Ph.D. Dissertation, Universite' des sciences et techniques du Languedoc, Montpellier, France.

Mandal, S. C., Maity, T.K., Das, J., Saba, B.P. and Pal, M. 2000. Anti-inflammatory evaluation of *Ficus racemosa* L. leaf extract. *Journal of Ethnopharmacology* 72: 87-92.

Mandal, S. C. and Kumar, C.K. 2002. Studies on anti-diarrhoeal activity of *Ficus hispida* leaf extract in rats. *Fitoterapia* 73: 663-667.

Moore, J.C., Hatcher, M.J., Dunn, A.M. and Compton, S.G. 2003. Fig choice by the pollinator of a gynodioecious fig: selection to rush, or intersexual mimicry? *Oikos* 101: 180-186.

Nefdt, R.J.C. 1989. Interactions between fig wasps and their host figs. M.Sc Thesis, Rhodes University, South Africa.

Nefdt, R.J.C. and Compton, S.G. 1996. Regulation of seed and pollinator production in the fig-fig wasp mutualism. *Journal of Animal Ecology* 65: 170–182.

Nilsamranjit, S. 1986. *A study on morphology, anatomy and growth of two cultivars of the common fig (Ficus carica* L.*) in the Highlands of Thailand.* M.S. Thesis (Horticulture), Graduate school, Kasetsart University, Bangkok.

Noort, S.V. and Rasplus, J.Y. 2005a. *Introduction to Ficus (fig trees).* (Online), Available: http://www.figweb.org/Ficus/introduction/index.htm (25 February 2006).

Noort, S.V. and Rasplus, J.Y. 2005b. *Classification of fig wasps.* (Online), Available: http://www.figweb.org/Fig_wasps/Classification/index.htm (25 February 2005).

O' Brien, B. 2008. *The life of Buddha.* (Online), Available: http://buddhism.about.com/od/lifeofthebuddha/a/buddhalife.htm). (25 May 2008).

Otero, J.T. 2002. Flower style length and seed production in two species of *Ficus* (Moraceae) on Puerto Rico. *Caribbean Journal of Science* 38 (3-4): 249-251.

Peh, K. and Chong, F. 2003. Seed dispersal agents of two *Ficus* species in a distributed tropical forest. *Ornithol. Sci.* 2: 119-125.

Phengklai, C. 1996. *A preliminary survey of plants diversity at Doi Inthanon.* A symposium on plant resources of the Himalayan foothills. Queen Sirikit Botanic Garden, 18-19 November 1996.

Phromthep, V. 1985. *Survey of cauliflorous plants in some areas of Changwat Chiang Mai and Sakol Nakhorn.* M.S. Thesis (Biology), Graduate school, Chiang Mai University, Chiang Mai.

Pitkin, B.R. 2004. *Notes on Families : Agaonidae.* (Online), Available: http://www.nhm.ac.uk /entomology/chalcidoids/agaonidae.html. (20 December 2004).

Ponpim, Y. 1996. *Ethnobotany of the hill tribes in Kaenoy's and Nongkheuw's Royal project in Chiang Mai.* M.S. Thesis (Biology), Graduate school, Chiang Mai University, Chiang Mai.

Rahuman, A.A., Venkatesan, P., Geetha, K., Gopalakrishnan, G., Bagavan, A. and Kamaraj, C. 2008. Mosquito larvicidal activity of gluanol acetate, a tetracyclic triterpenes derived from *Ficus racemosa* L. *Parasitol Res.* 103: 333–339.

Rakkien, N. Sripet, S., Chantarasuwan, B., Jaroensutasinee, M. and Jaroensutasinee, K. 2007. *Species, abundance, feeding location and feeding time of frugivores on dye fig (F. tinctoria Forst.f. subsp. gibbosa (Blume) Corner) at Khao Nan National Park.* The 11th BRT Annual Conference, 15-18 October, 2007 Napalai, Udonthani. p 47.

Ramirez, B.W. 1976. Germination of seed of new world *Urostigma* (*Ficus*) and *Morus rubra* L. (Moraceae). *Rev. Biol. Trop.* 24: 1-6.

Royal Forest Department. *Forestry statistics.* (Online), Available:http://www.forest.go.th/stat49/stat2549, (20 May 2008).

Santisuk, T. 2007. *Vegetation types in Thailand.* Bangkok: Arunkanpim.

Shanahan, M., Compton, S.G., So, S. and Corlett, R. 2001a. Fig-eating by vertebrate frugivoes: A global review. *Biological Reviews* 76: 529-572.

Shanahan, M., Harrison, R.D., Yamuna, R., Boen, W. and Thornton, W.B. 2001b. Colonization of an island volcano, Long Island, Papua New Guinea and an emergent island, Motmot, in its caldera lake. V. Colonization by figs (*Ficus* spp.), their dispersers and pollinators. *Journal of Biogeography* 28: 1365-1377.

Smitinand, T. 2001. *Thai plants names: Tem Smitinand (Revised Edition).* The Forest Herbarium Department. Bangkok: Prachachon Ltd.

Song, Q., Young, D., Zhang, G. and Young, C. 2001. Volatiles from *Ficus hispida* and their attractiveness to fig wasps. *Journal of Chemical Ecology* 27 (10): 1929-1941.

Sri-Ngernyuang, K., Kanzaki, M. and Itoh, A. 2007. Seed production and dispersal of four Lauraceae species in a tropical lower montane forest, Northern Thailand. *Mj. Int. J. Sci. Tech.* 01: 73-87.

Srisanga, P. 2005. *Biodiversity of vascular plants on Doi Phu Kha National Park.* PhD thesis (Biology), Graduate school, Chiang Mai University, Chiang Mai.

Tangtrakul, T., Tarachai, Y., Hongvittayakorn, P. Prokati, V. and Preechawattanakorn, P. 2001. *Medicinal plant used by Ban Pong people Sansai district, Chiang Mai province.* The 3rd Maejo University Annual Conference, 26-27 July, 2001. Maejo University, Chiang Mai, Thailand; pp. 378-388.

Tanming, W. and Chantaranothai, P. 2007. *A taxonomic revision of the genus Ficus L. in Northeastern Thailand.* The 11th BRT Annual Conference, 15-18 October, 2007 Napalai, Udonthani. p. 193.

Tovaranonte, J. 1998. *Ethnobotany of Tai Lue, Hmong and Yao in Some Areas of Nan Province*. M.S. Thesis (Biology), Graduate school, Chiang Mai University, Chiang Mai.

Triola, M.F. 2004. *Elementary Statistics.* USA: Creg Tobin Publisher.

Verkerke, W. 1989. Structure and function of the fig. *Experientia* 45: 612-622.

Vinson, J.A. 1999. The functional food properties of figs. *Cereal Foods World* 44 (2): 82-87.

Wang, R., Yang, J. and Yang, D. 2005. Seasonal Changes in the Trade-off Among Fig-supported Wasps and Viable Seeds in Figs and Their Evolutionary Implications. Journal of Integrative Plant Biology Formerly *Acta Botanica Sinica* 47 (2): 144–152.

Ware, A.B., Compton, S.G., Kay, P.T. and Noort, V. S. 1993. Fig volatiles: their role in attracting pollinators and maintaining pollinator specificity. *Plant. Syst. Evol.* 186: 147-156.

Weiblen, G.D. Yu, D.W. and West, S.A. 2001. Pollination and parasitism in functionally dioecious figs. *Proceedings of the Royal Society, London (B)* 268: 651-659.

Weiblen, G.D. 2002. How to be a fig wasp. *Annu. Rev. Entomol.* 47:299–330.

Wiebes, J.T. 1979. Co-evolution of figs and their insect pollinators. *Ann. Rev. ecol. Syst.* 10: 1-12.

Wiebes, J.T. 1994. *The Indo-Australian Agaoninae (pollinators of figs).* Amsterdam: North-Holland.

Winsor, D.M., Morrison, D.W., Estribi, M.A. and Leon, B.de. 1989. Phenology of fruit and leaf production by 'strangler' figs on Barro Colorado Island, Panama. *Experientia* 45: 647-653.

Yang, D., Peng Y., Song, Q., Zhang, G., Wang, R., Zhao, T. and Wang, Q. 2002. Pollination biology of *Ficus hispida* in the tropical rainforests of Xishuangbanna, China. *Acta Botanica Sinica* 44 (5): 519-526.

Zhang, G., Song, Q. and Yang, D. 2006. Phenology of *Ficus racemosa* in Xishuangbanna, Southwest China. *Biotropica* 38 (3): 334-341.

Zhekun, Z. and Gilert, M. 2003. *Flora of China.* 5: 21-73. (Online) Available: http://flora.huh.harvard.edu/china/mss/volume05/Moraceae.pdf (09 April 2003).

APPENDIX

Terminology

'**Gynodioecious**' is referred to the fig species with male and female trees in the population. Male trees (caprifigs) bear 'male' syconia containing pollen-bearing male flowers and short –style female flowers. The ovaries of short style female flowers often contain a male or female wasp larva if eggs were deposited inside them. Female tree only bear female flowers syconia containing seed bearing long style female flowers and no male flowers. About half the world's 1000+ fig species are gynodioecious, short-style and long style female flowers in the same syconium. (Armstrong and Disparti, 1998)

'**Pollen basket**' pollen collecting device: A special-adapted collective cavity or bristles on female wasp where pollen is purposively deposited before leaving the male (caprifig) syconium. (Armstrong and Disparti, 1998)

'**Keystone**' defined a keystone species as "one whose impact on its community or ecosystem is large and disproportionately large relative to its abundance" (Power, 1966 in Shanahan *et al.*, 2001)

'**Foundress**' is the female pollinator with pollen carrying

'**Bladders**' are the developed gall flowers without wasps that caused by the premature death of wasp eggs or larvae (Gailil & Eisikowitch, 1971)

Terminology of fig (Berg and Corner, 2005)

'**gall-figs**' for the functionally male syconia with the ovaries only used breeding sites for fig insects and with a wall at maturity often less fleshy and usually color different from the ‘seed figs’, remaining green or with paler colors, generally less attractive to frugivorous animals;

‘seed-figs’ for the functional female syconia with the ovaries unsuitable used as breeding site for fig insects and with a wall at maturity more fleshy and darker colored than that of ‘gall figs’ and is attractive for frugivorous animals;

‘gall-fruit’ for the fruit developed from ovaries in which the insects develop and of with the pericarp develop differently.

Climatology of Chiang Mai between 2006 and 2007

month/ 2006	temperature				humidity (%RH)		rain
	max	min	average	max	min	average	month(mm)
January	30.14	14.76	21.21	97.23	44.06	75.10	0.00
February	32.88	17.46	24.68	90.80	38.40	64.70	0.00
March	36.21	19.91	27.75	81.30	33.70	56.30	18.00
April	36.72	21.89	28.43	88.40	44.00	67.30	206.70
May	33.42	21.74	26.53	96.10	62.30	81.70	219.50
June	34.05	23.20	27.62	97.10	63.00	83.20	180.40
July	30.63	23.60	26.37	97.60	74.30	88.00	269.30
August	30.68	23.39	26.05	98.60	75.00	90.60	341.40
September	32.17	23.38	26.70	98.00	64.40	85.80	194.80
October	31.61	21.97	25.84	98.40	62.50	84.90	69.90
November	31.57	18.19	24.00	98.10	50.30	77.90	0.00
December	29.10	16.10	21.89	95.40	46.50	73.20	0.00
January	29.75	14.49	22.10	94.10	40.90	70.20	0.00
February	32.35	15.53	23.40	85.90	33.70	59.10	0.00
March	35.75	18.37	26.57	74.80	29.10	51.50	0.00
April	36.66	23.31	29.62	79.00	38.20	58.00	56.00
May	31.48	23.29	26.52	95.80	67.00	84.80	393.50
June	33.08	24.26	27.85	95.40	62.50	81.70	130.10
July	31.45	24.07	27.04	95.20	65.20	82.60	74.60
mean	32.62	20.47	25.80	92.49	52.37	74.56	113.38

Curriculum Vitae

Name Mrs. Yaowanit Tarachai

Date of Birth February 23, 1969

Education Background

1990 Bachelor of Science (Agriculture), Khon Khaen University

Department of Entomology, Faculty of Agriculture

1996 - Master of Science (Biology), Chiang Mai University

Department of Biology, Chiang Mai University

Scholarships The Commission on Higher Education of Thailand and Maejo University

Graduate School of Chiang Mai University, Chiang Mai, Thailand

The TRF/BIOTEC Special Program for Biodiversity Research and Training grant

Experience

1997-present Lecturer,

Faculty of Architecture and Environmental Design, Maejo University, Chiang Mai

Publications

1. Tarachai, Y., Compton, S.G. and Trisonthi, C. 2006. *Functional relationships between a fig tree and its pollinators.* Proceeding of the 7th International Symposium on fig-fig wasp biology, 23-26 July 2006, Xishuangbanna, China.

2. Tarachai, Y., Sukumalanand, P., Wangpakapattanawong, P., Compton, S.G. and Trisonthi, C. 2007. *Taxonomy of some figs and their pollinators.* The 11th BRT Annual Conference, 15-18 October 2007, Napalai, Udonthani.
3. Tarachai, Y., Compton, S.G. and Trisonthi, C. 2008. The benefits of pollination for a fig wasp. *Symbiosis*, 45: 29-32.
4. Tarachai, Y., Sukumalanand, P., Wangpakapattanawong, P., Compton, S.G. and Trisonthi, C. 2008. *Co-evolution of Ficus racemosa L. and its pollinator.* Proceedings of the 10th year anniversary Mae Fha Luang conference, 26-28 November 2008, Mae Fah Luang University, Chiangrai.