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 17º 15´ N - 20º 16´ N and longitude 98º 03´ E - 99º 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.

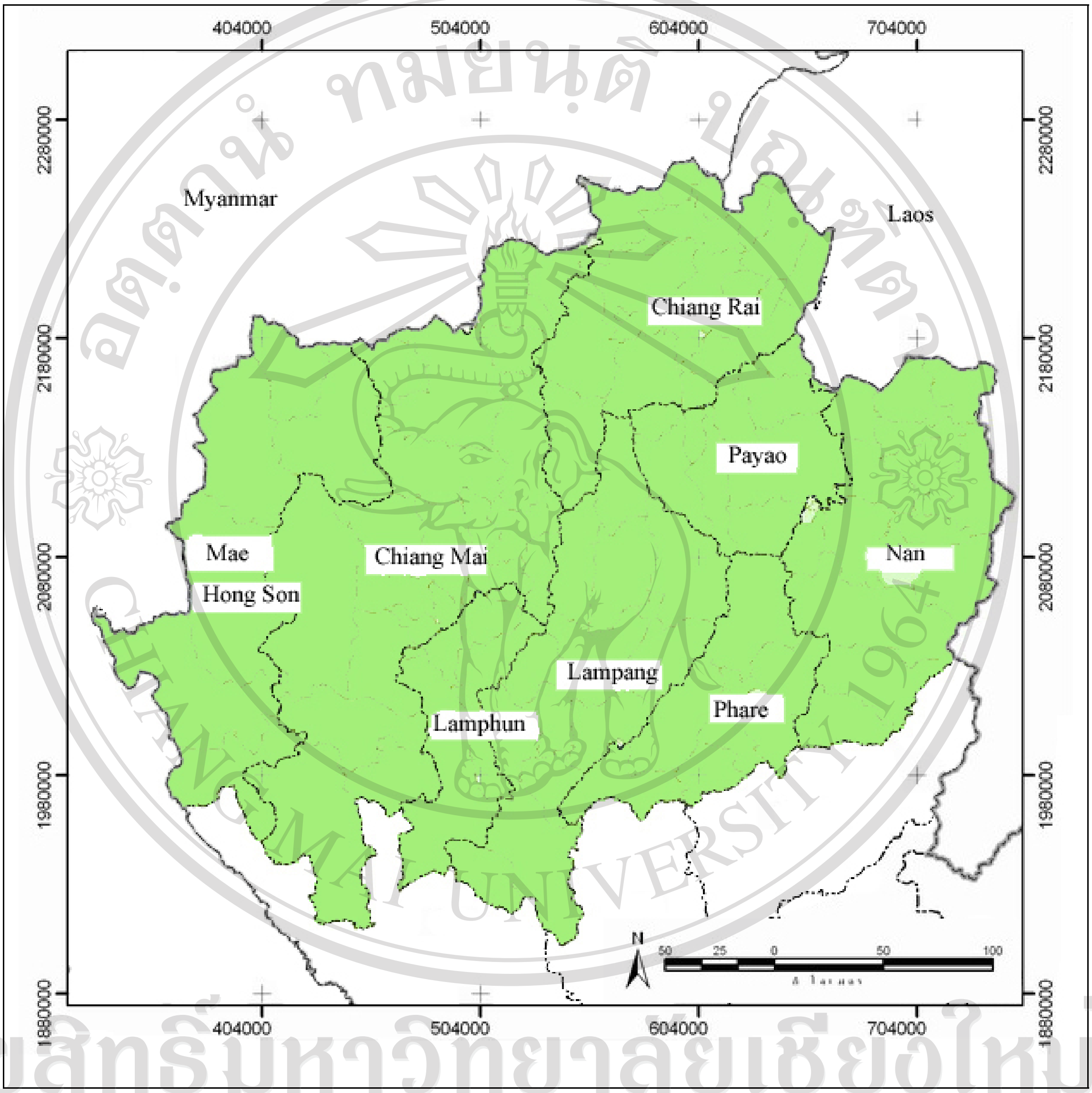


Figure 2.1 Map of Northern Thailand (Department of Geography, Faculty of Social Sciences, Chiang Mai University, 2007)

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)

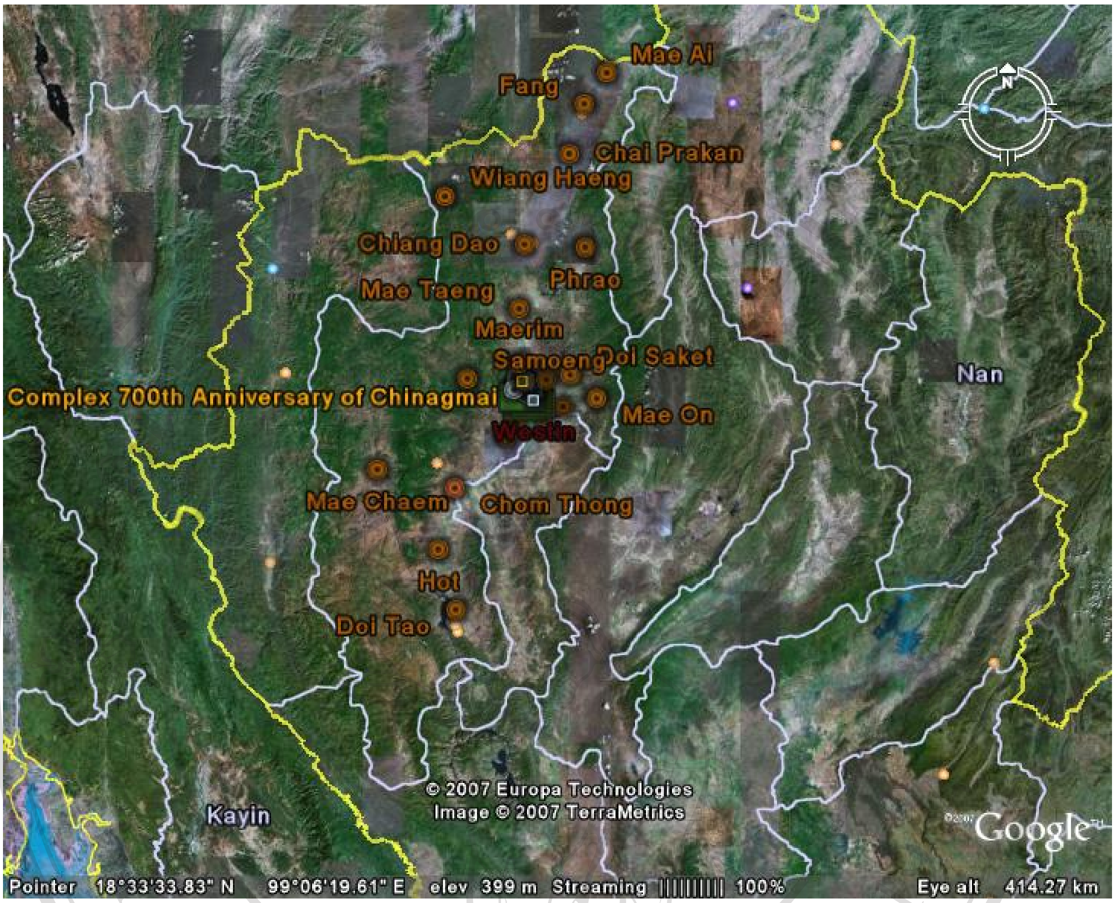


Figure 2.2 Map of geography and topology of Chiang Mai (www.googleearth.com, 6 July 2007).

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 º C (Figure 2.3) and colder in the hills, sometimes as low as 0 º C on the highland.

2) Hot and dry season (hot); during mid of February to mid May, temperature rises to 36-40 º 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.

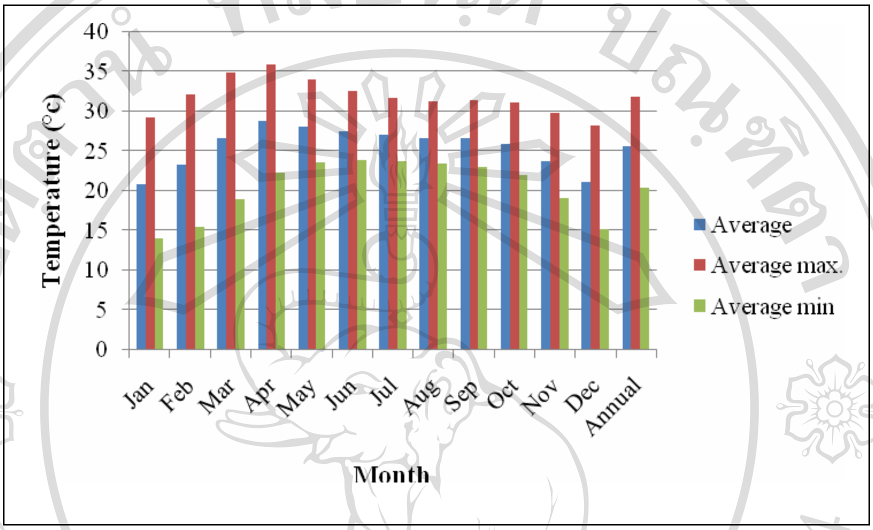


Figure 2.3 Temperature (ºC) of Chiang Mai from 1971-2000 (30 years) (Department of Meteorology, Chiang Mai, 2007)

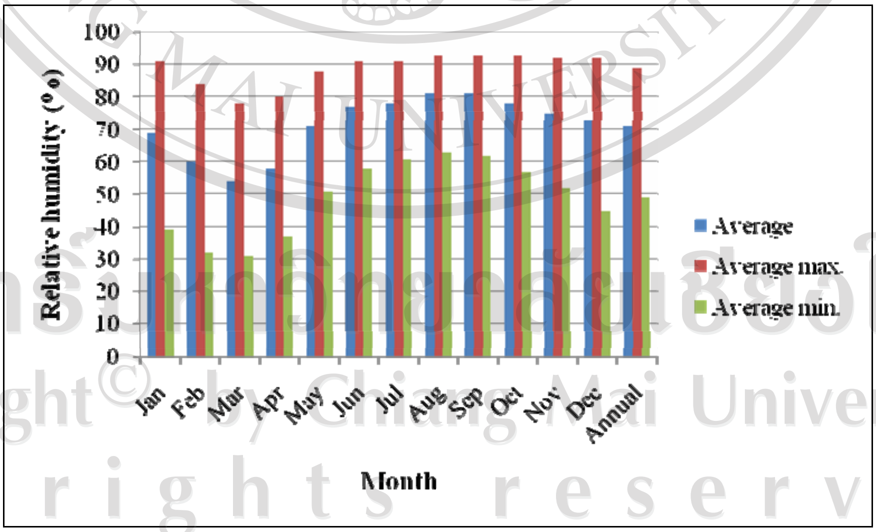


Figure 2.4 Relative humidity (%) of Chiang Mai from 1971-2000 (30 years) (Department of Meteorology, Chiang Mai, 2007)

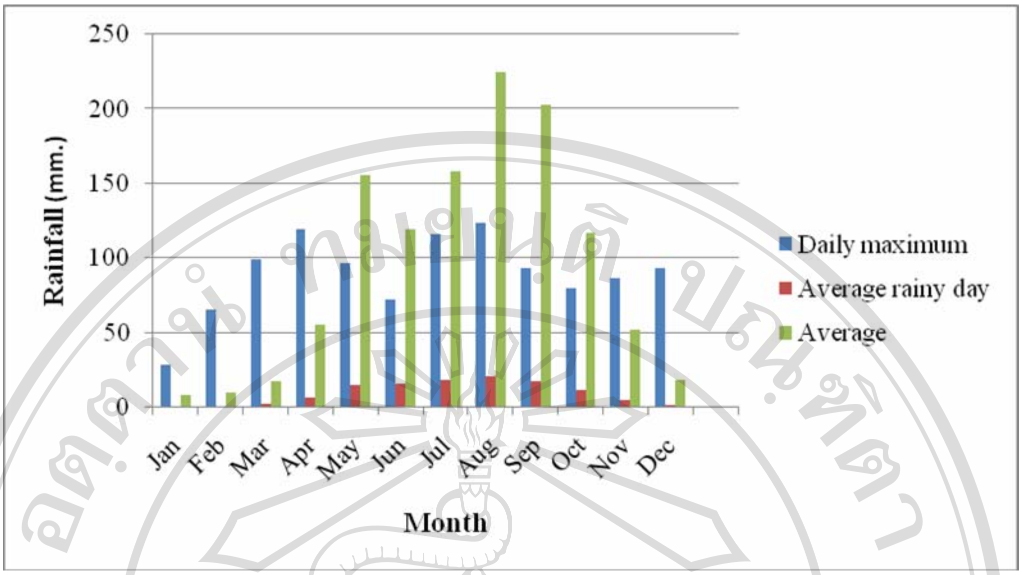


Figure 2.5 Rainfall (mm) of Chiang Mai from 1971-2000 (30 years) (Department of Meteorology, Chiang Mai, 2007)

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).

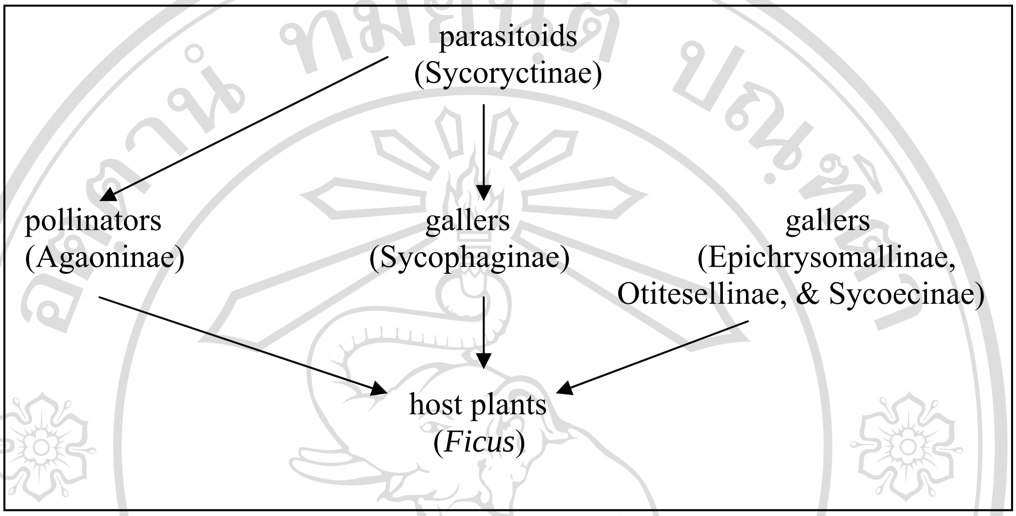


Figure 2.6 Trophic relationships among figs and fig wasps. Agaonid subfamilies include pollinators, gallers, and parasitoids (after Weiblen, 2002).

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).

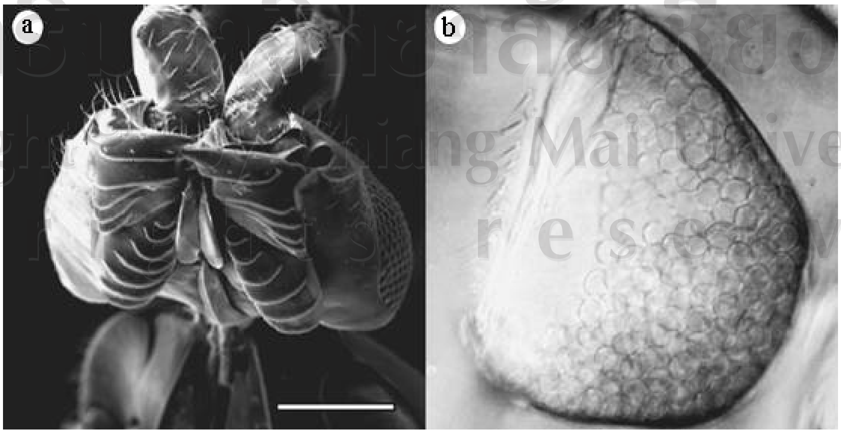


Figure 2.8 *a*. Ventral view of the female head of *Kradibia ohuensis* showing mandibular appendage with six lamellae (scale = 0.1 mm), *b.* Pollen pocket of *Ceratosolen kaironkensis* containing *Ficus microdictya* pollen grains (after Wieblen, 2002).

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).

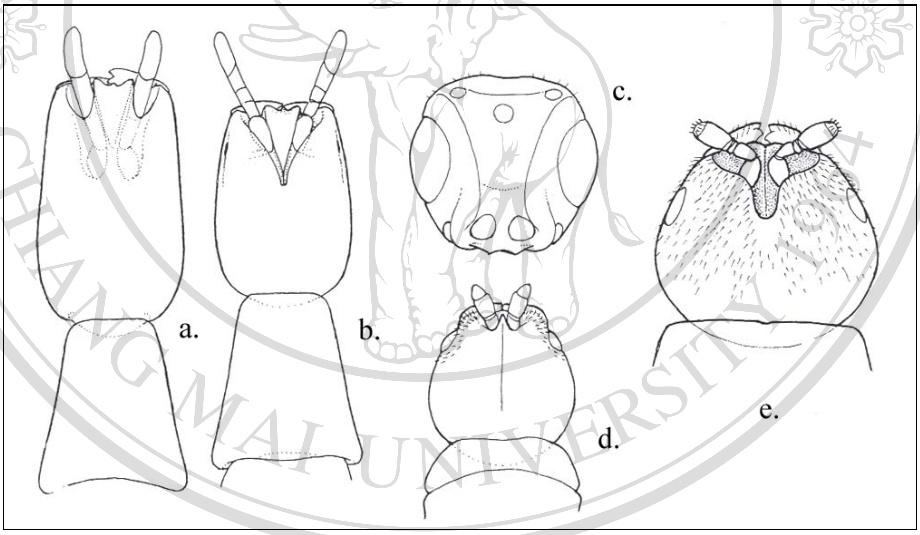


Figure 2.9 *a. Ceratosolen indigenus*; male head with pronotum, *b. C. vissali*; male head with pronotum, *c. Kradibia wassae*; female head, *d. Blastophaga vidua*; male head and *e. B. psense*; male head (after Bouček, 1988).

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).

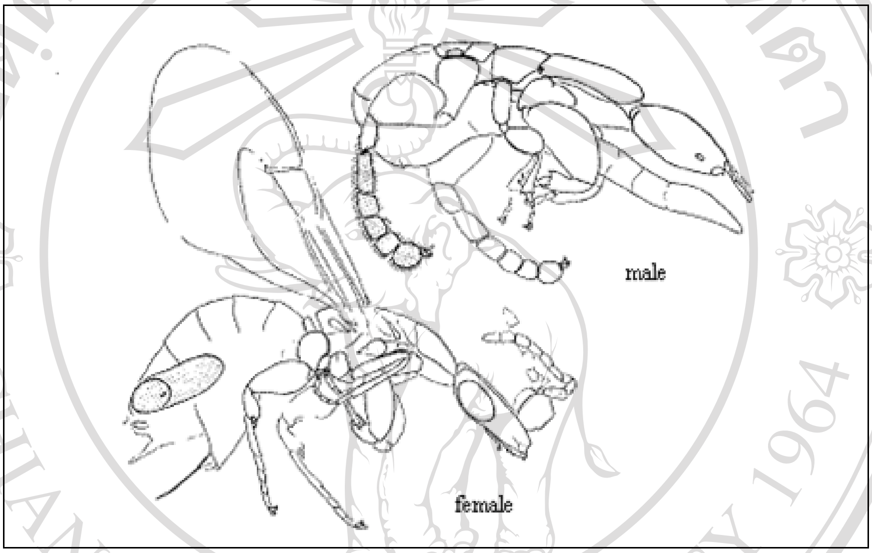


Figure 2.10 *Ceratosolen dentifer* Wiebes, female (left)-pollen pocket in the mesosternum of the thorax and male (right)-with the large hirsute hind legs (after Wiebes, 1979).

2.5 BIOLOGY OF FIG AND FIG WASPS

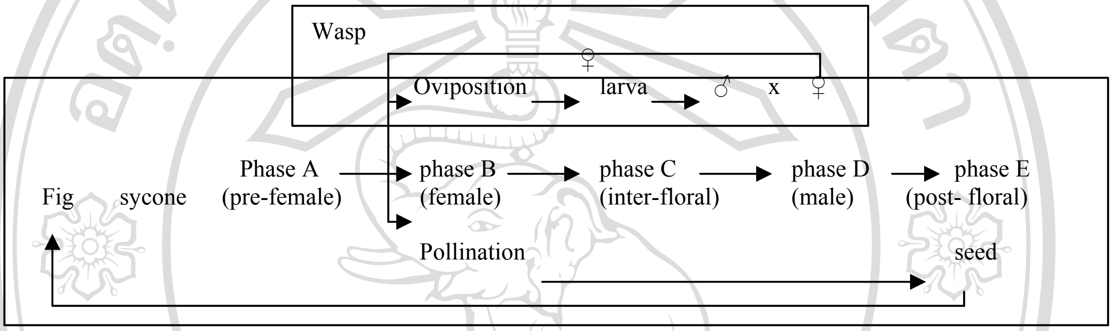
Figs and their pollinators were recorded as fossil beyond 90 million years ago (Machado *et al*., 2001). The symbiosis figs and their pollinating wasps (Agaoninae) form is a typical co-evolution study. They cannot live and reproduce without each other. Although figs can grow individually, their seeds 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

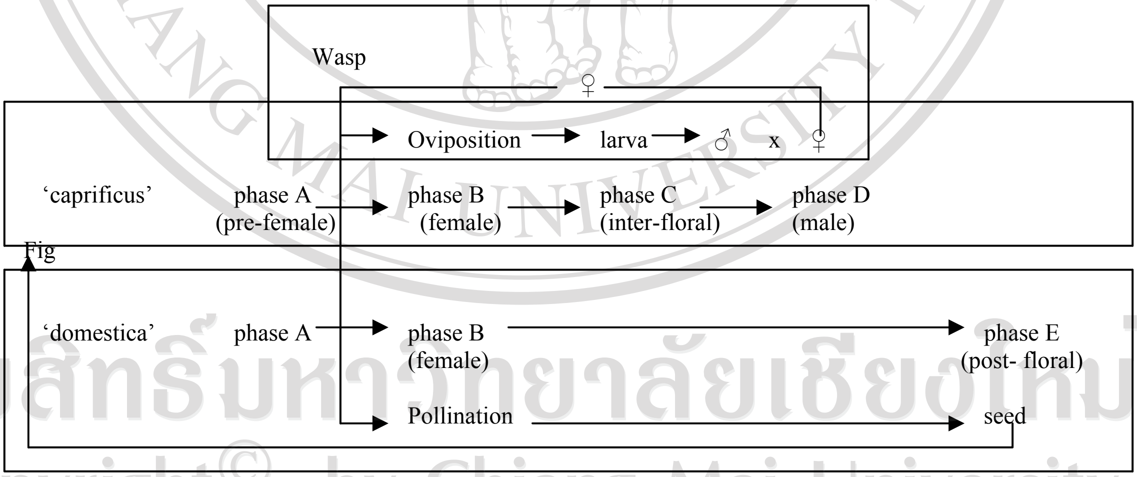
The fig inflorescence is called "fig" or "syconium" with the fruit-like shape. This character is evolved from receptacle. Inside the syconium, lots of tiny flowers born on the inner side. Inside each syconium, it is composed of 50-7,000 unisexual flowers (Endress, 1994). In the development of the syconium,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

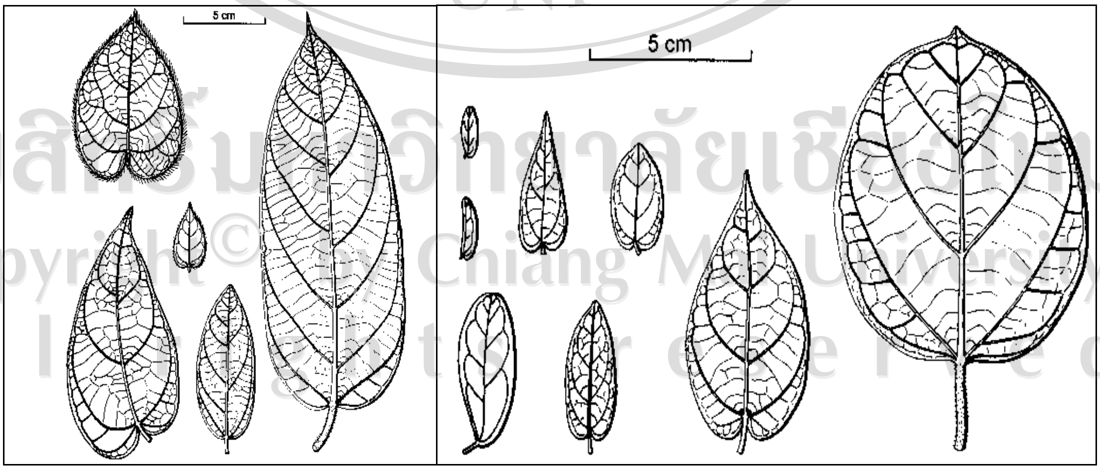


Figure 2.13 Variation on size, texture and shape of fig leaves (after Berg and Corner, 2005).

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)

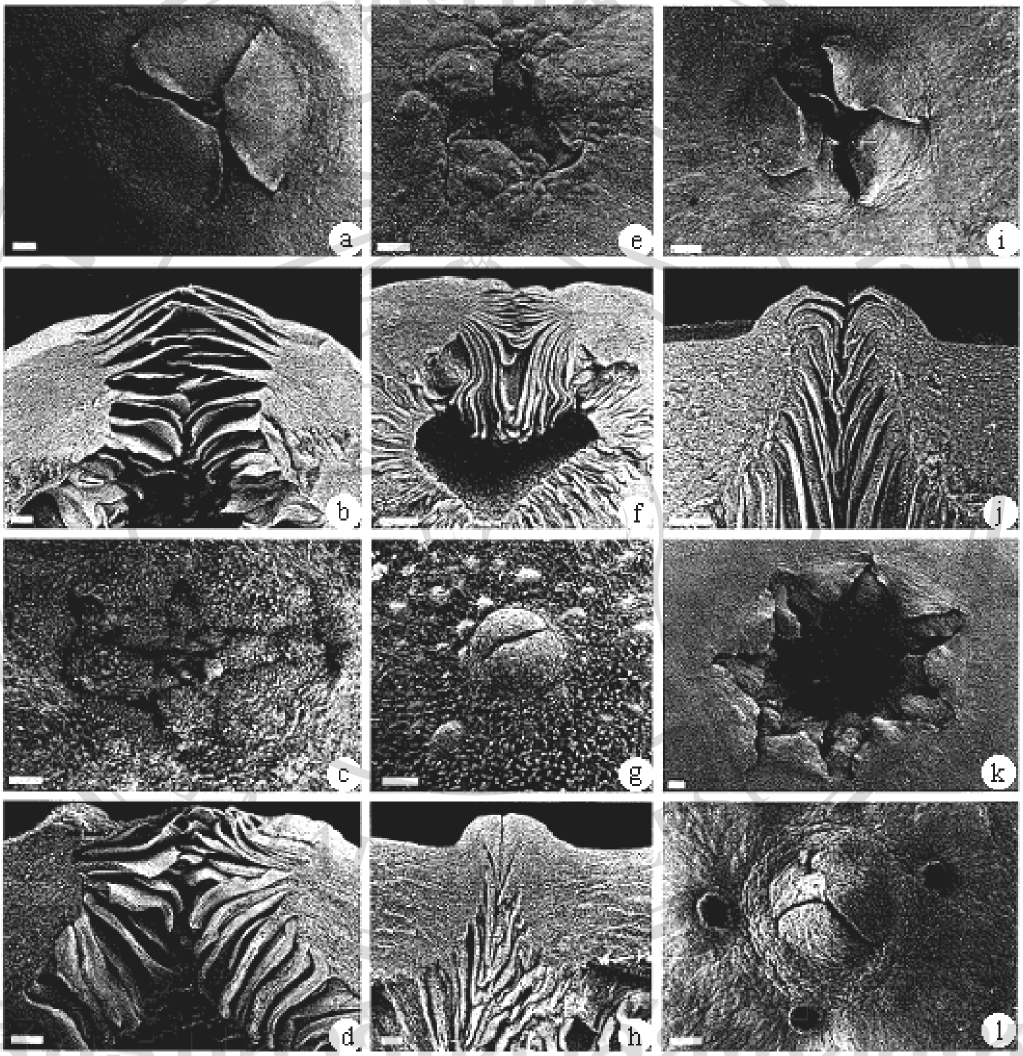


Figure 2.14 Top view and longitudinal section of various types of ostiole and ostiolar bracts; *a,b* subgenus *Ficus*; *c,d* *Sycidium*; *e,f Sycomorus*; *g,h Urostigma* section *Galoglychia*; *i,j,k* section *Pharmacosycea*; *l Urostigma* section *Americana*; bar indicates 500 µm. (after Verkerke, 1989)

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.

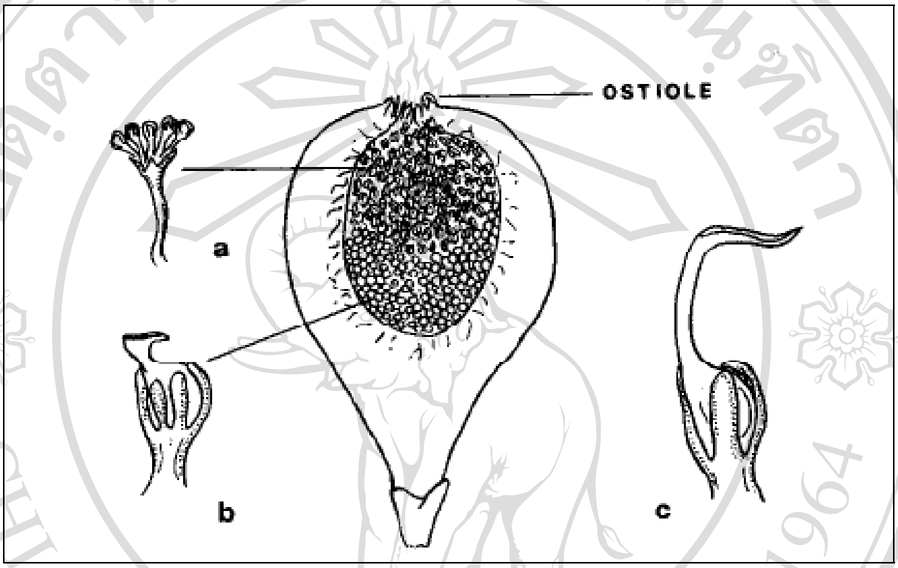


Figure 2.15 Longitudinal fig sycone, *a.* staminate and pistillate flowers; *b.* short-styled flower (gall) and *c.* long-styled flower (after Wiebes, 1982 in Berg and Wiebes, 1992).

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.

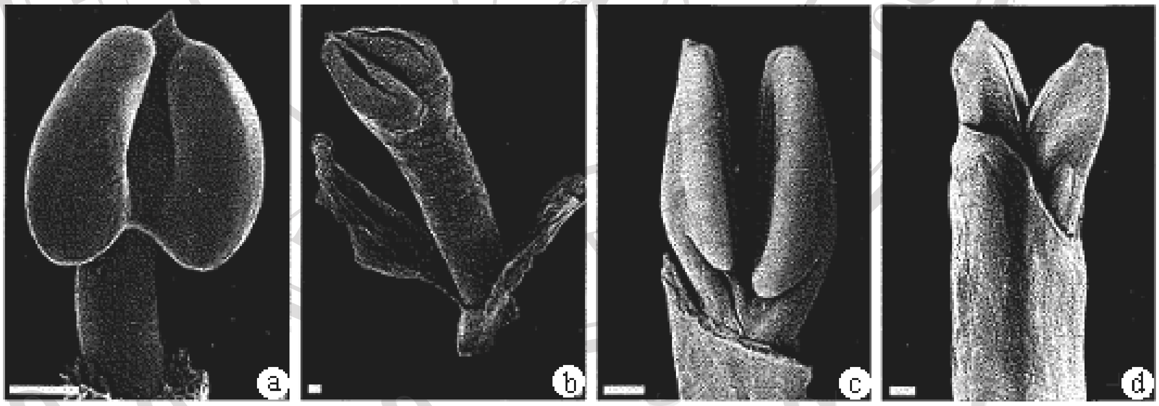


Figure 2.16 Staminate flower (perianth removed); *a, b Urostigma* section *Galoglychia* (perianth removed), *c* section *Pharmacosycea*, *d* section *Sycomorus*; bar indicates 200 µm (after Verkerke, 1989).

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).

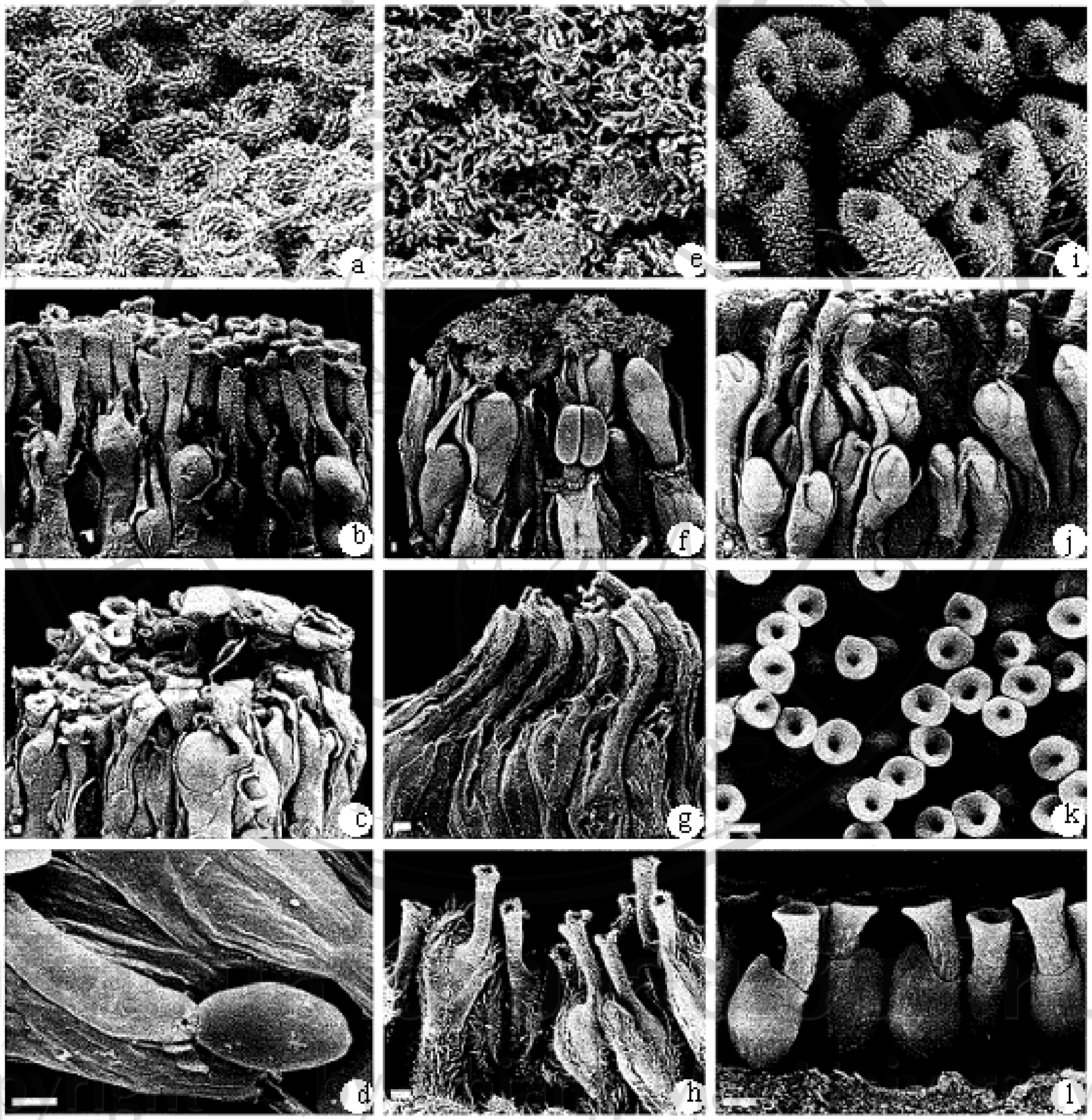


Figure 2.17 Female flower; surface and lateral view; *a-f* monoecious figs; *g-l* gynodioecious figs; *a-d* section *Sycomorus*, *c* ovipositing *Ceratosolen* spp.; *d* germinating pollen grain; *e-f Urostigma* section *Galoglychia*; *g,h Sycidium*, seed flower and gall flower; *I,j Neomorphe*, seed 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).

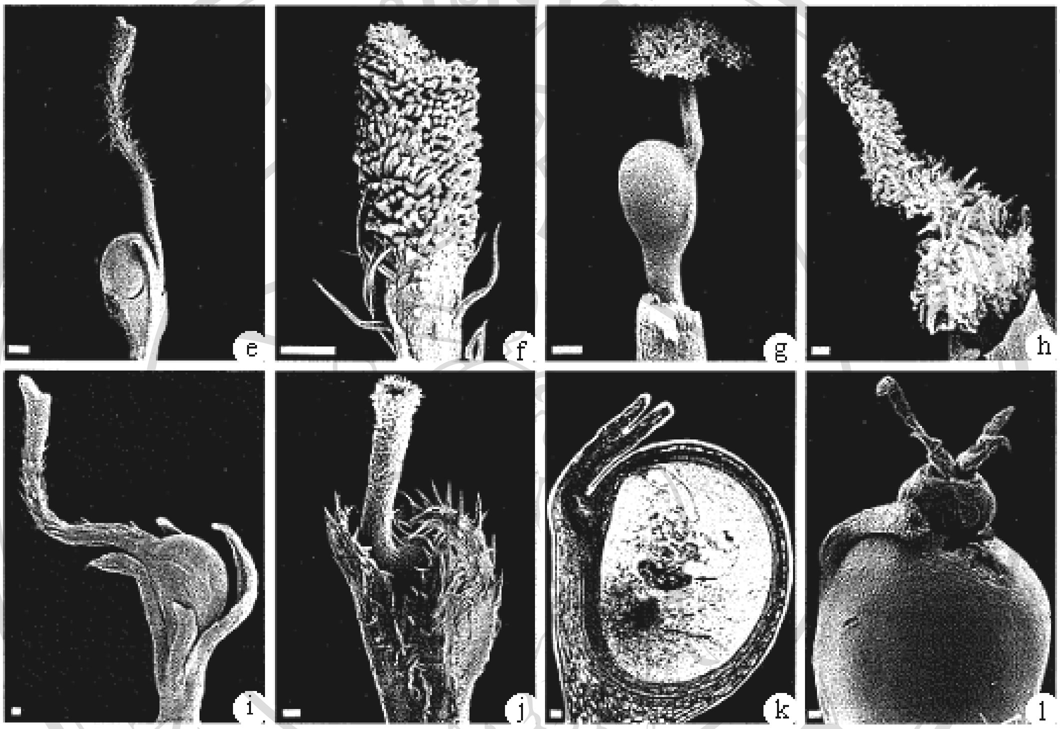


Figure 2.18 Pistillate flowers; *e,f Neomorphe* seed flower, and detail of stigma, *g,h Urostigma* section *Galoglychia*, short-styled flower (perianth removed); and stigma from the long-styled flower, *i-l Sycidium*; *i* seed flower, *j* gall flower; *k* gall flower, arrow indicating wasp larva, *l 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)

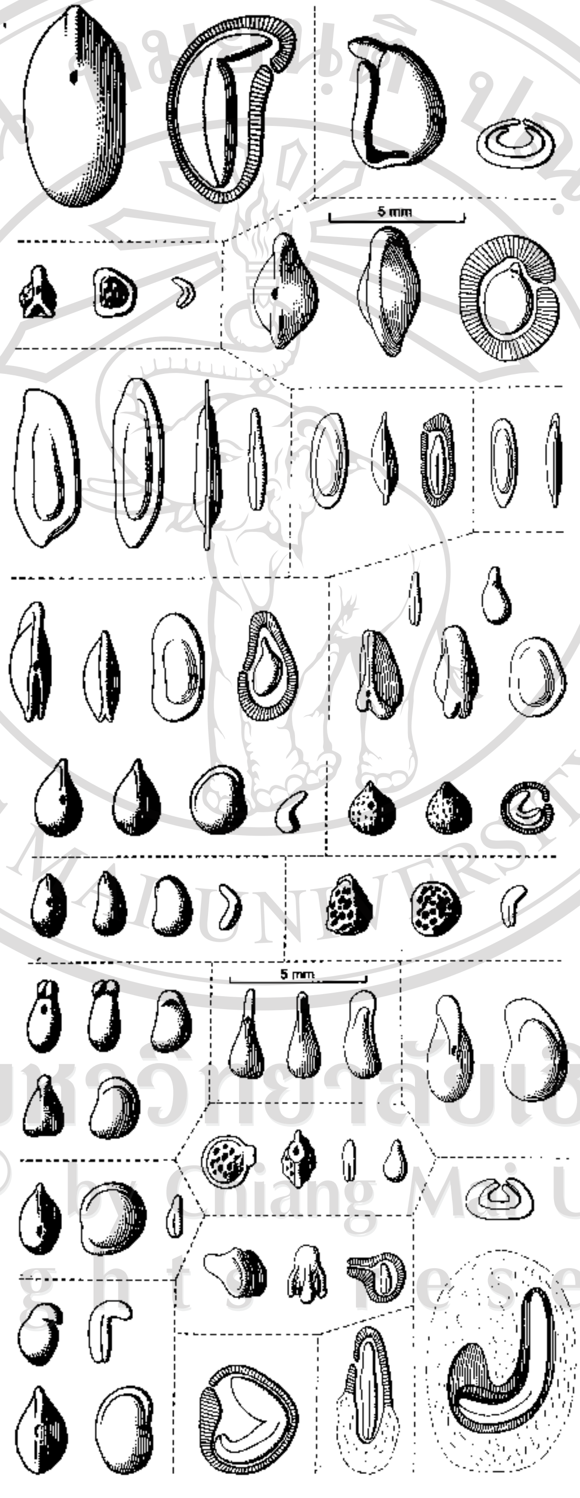

5 mm
5 mm

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.

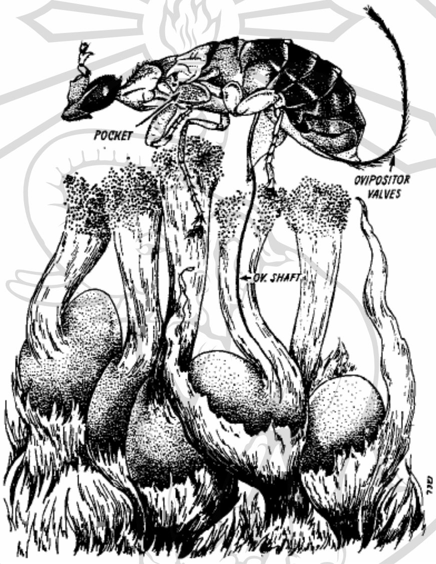


Figure 2.20 *Ceratosolen arabicus* Mayr and its host, *Ficus sycomorus* during oviposition and pollination. (after Galil and Eisikowitch, 1968)

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).

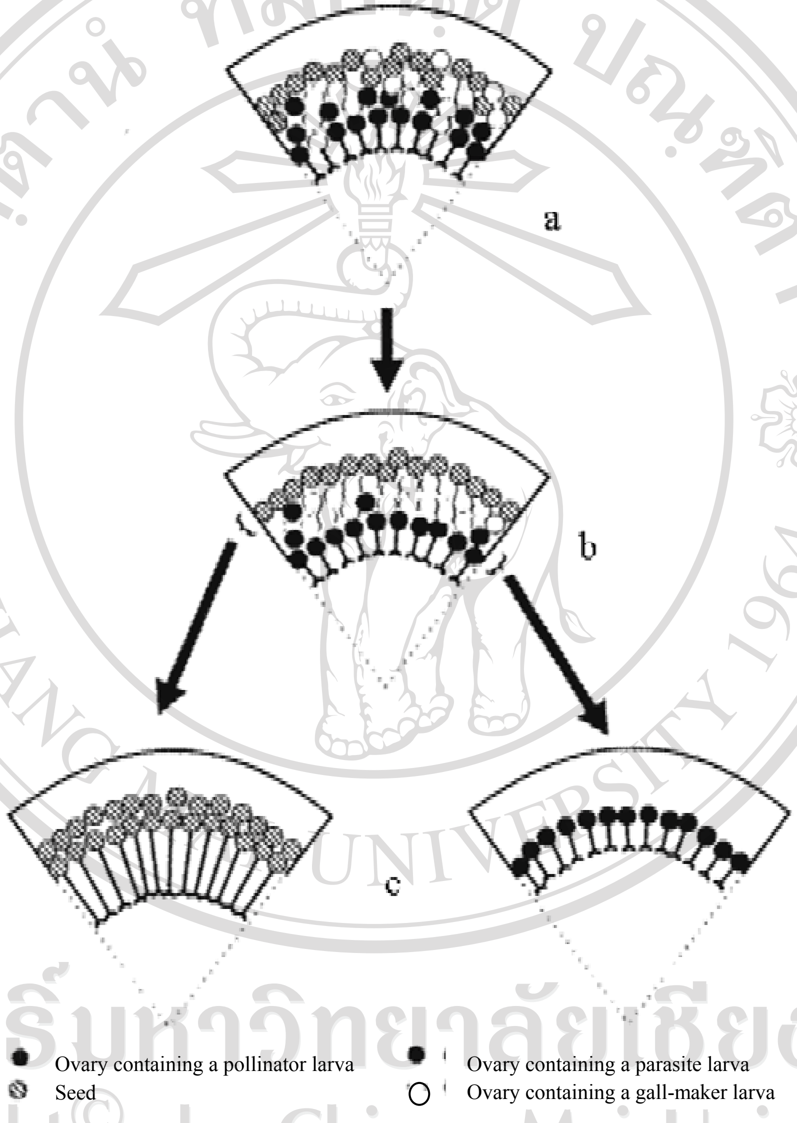


Figure 2.21 The evolution pattern of oviposition in dioecy and monoecy fig tree. *a*. pattern in monoecy figs, b. representation of non pollinating wasp in medium layer and c. evolution towards dioecy figs which separate to male and female trees (after Kerdelhue′ and Rasplus, 1996)

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*)

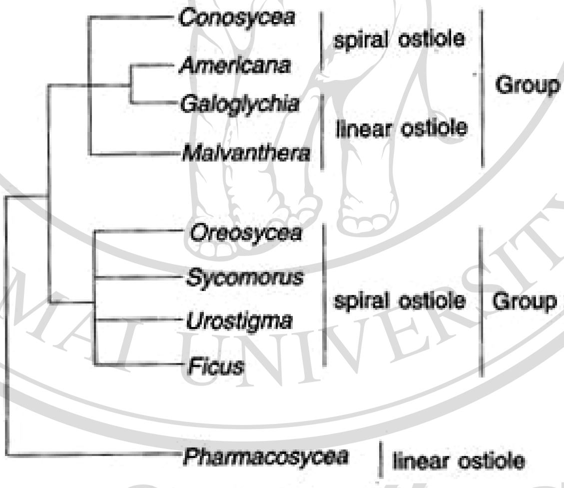


Figure 2.22 A molecular phylogeny of *Ficus*, two monophyletic groups are defined; group 1, group 2 and the outgroup, section *Pharmacosycea*. Spiral ostioles seem to have evolved three times independently (after Kjellberg *et al*., 2005).

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).