Structuring mechanisms of the *Crematogaster-Macaranga* ant-plant association: A combined ecological and phylogenetic approach

Dissertation

at the Faculty of Biology

Johann Wolfgang Goethe-University Frankfurt

submitted by

Heike B. Feldhaar

Frankfurt am Main

Frankfurt am Main, 2002

Strukturierungsmechanismen der *Crematogaster-Macaranga* Ameisen-Pflanzen Assoziationen: ein kombinierter ökologischer und phylogenetischer Ansatz

Dissertation

zur Erlangung des Doktorgrades
der Naturwissenschaften

vorgelegt beim Fachbereich Biologie

der Johann Wolfgang Goethe-Universität Frankfurt am Main

Heike B. Feldhaar

aus

Frankfurt am Main

Frankfurt am Main, 2002

Vom Fachbereich

.....der

Johann Wolfgang Goethe – Universität als Dissertation angenommen.

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Heike Feldhaar

1 Introduction

”If we are to gain insights into the nature of selective forces, it must come, I think, from a study of ecology. In particular, it must come from a study of the coevolution of interacting species, because the main selective forces acting on a species are likely to come from changes in its competitors, its predators, and its parasites” (Maynard Smith, 1998), and, one could add, its symbionts.

Ecological interactions between species have been recognized as an important evolutionary factor driving speciation (e.g., Schluter, 2000; Schluter, 2001). Mutualistic ant-plant associations are a common phenomenon in tropical ecosystems. Obligate ant-plants (or myrmecophytes) provide nesting space (domatia) and often also food for ants. In exchange the ant inhabitants effectively protect their host plants against herbivory or climber infestation (for reviews see e.g. Buckley, 1982; Beattie, 1985; Hölldobler and Wilson, 1990; Davidson and McKey, 1993b).

The most prominent ant-plant system in the palaeotropics consists of the pioneer tree genus *Macaranga* (Euphorbiaceae) and its manifold associations with ants, mainly from the genus *Crematogaster* subgenus *Decacrema*. *Macaranga* plants are also colonized by at least four species of *Camponotus* and one species of *Crematogaster* from a different subgenus than *Decacrema* (Fiala et al., 1996; Maschwitz et al., 1996; Federle et al., 1998a and 1998b; Fiala et al., 1999).

The various types of interaction in this ant-plant complex and its considerable degree of radiation concerning the *Macaranga* host plants as well as the partner ants and especially the *Decacrema* species offer an exceptional model system for studying the processes of speciation and radiation in mutualistic systems in general.

For most of the important and common ant-plant genera worldwide the geographic distribution patterns as well as the specificity of the associations are known (*Macaranga*: Fiala et al. 1999; *Cecropia*: Longino,

1989, 1991; Ayala et al., 1996; Yu and Davidson 1997; *Acacia*: Janzen, 1973; Ward, 1993; *Leonardoxa*: McKey, 1984; *Cladomyrma* spp. complex and their respective host plants, Agosti et al., 1999; *Triplaris* and *Tachigali*: Ward, 1999). These associations are rarely species-specific in a sense that each species of ants has only one specific plant partner and vice versa. Often ”guilds” of unrelated but ecologically similar ants or several related ants interact with a ”guild” of host-plants that show morphological and physiological similarities (Ward, 1991; Davidson and McKey, 1993a and 1993b; Chenuil and McKey, 1996; Agosti et al., 1999; Fiala et al., 1999; Ward, 1999). This also holds true for the associations between *Macaranga* and their main partner ants from the genus *Crematogaster* subgenus *Decacrema*: Each specific partner ant is usually associated with at least two to several *Macaranga* species (overview Fiala et al., 1999). The colonization patterns usually but not always reflect existing taxonomic sections within the genus *Macaranga* (Fiala et al., 1999; Blattner et al., 2001). Nonetheless, colonization patterns are maintained in spite of a sympatric distribution of *Macaranga* species and often patchy occurrence of the respective host plant (Fiala et al., 1999) and therefore these associations may still be called highly specific.

However, to date little is known about the proximate as well as the ultimate factors leading to the recurring and non-random patterns of associations between *Crematogaster (Decacrema)* and their *Macaranga* host plants that were found in extensive studies on biogeography, ecology and specificity of the association (e.g. Fiala, 1996; Fiala et al., 1999; Moog et al., 2002; and references cited therein).

One possible explanation for the emergence of the recurring association patterns is that the ant and plant lineages have evolved in concert with one another. The patterns would then be the outcome of parallel cladogenesis. However, since species-specificity in the *Crematogaster* (*Decacrema*)–*Macaranga* association is not absolute, the associations might be the result of ‘diffuse cospeciation or coevolution’ (sensu Davidson and McKey 1993a). On the other hand biotic as well as abiotic ecological factors, e.g. inter- and intraspecific competition or habitat-preferences, may be the crucial driving force for the determination of the

ant-plant associations. Several lines of evidence suggest that ant populations are directly limited by their host plant populations, thus generating intra- and interspecific competition for nesting sites (e.g., Longino, 1989; Perlman, 1992; Yu and Davidson, 1997). Competition could restrict ant species to fewer plant partners than they are actually capable to colonize and could result in strong selection for traits specific for particular associations and local host plant populations.

The role of coevolution versus coadaptation (i.e. the match of characters of independent origins) in determining ant-plant associations is controversial (for an overview see Davidson and McKey, 1993b). The general outcome of recent studies on ant-plant associations is that similar mutualisms often evolved independently by de novo colonization , and host switching within established mutualistic systems appears to be more common than cospeciation (Ward, 1993; Ayala et al., 1996; Chenuil and McKey, 1996; Ward, 1999; Brouat et al., 2001b).

The successful colonization of a specific host plant by specific partner ants, that leads to the recurring and non-random association patterns found in host plant saplings, may underlie different selective forces than the maintenance of the associations. However, the most important fitness parameter -reproductive success- is dependent on the durability and maintenance of the obligate associations over time. The associations need to be stable at least until maturity of one or both partners is reached to ensure reproduction. To date knowledge of the development and temporal stability of the *Crematogaster–Macaranga* associations beyond establishment of the ant colony on young plants is sparse.

The aim of this study is to examine the factors leading to the observed association patterns by elucidating the evolutionary history of the *Crematogaster-Macaranga* association and distinguishing the relative roles of coevolutionary accommodation vs. ecological factors in determining the association patterns.

Since combining ecological data with a phylogeny inferred from molecular data is a powerful approach to studying the evolution of interacting lineages (Brooks and McLennan, 1991), this study comprises two different approaches for examining the patterns of the associations between *Crematogaster* ants of the subgenus *Decacrema* and their respective *Macaranga* host plants: First I investigated the temporal variation and dynamics of the most common *Crematogaster-Macaranga* associations. Life-history traits of the most common morphospecies of ants of the subgenus *Decacrema* were compared in relation to their host-plant species. To evaluate whether historical factors might be responsible for the specific patterns of associations found, knowledge of the phylogenetic relationships within the ant partners is paramount. The second approach is therefore a phylogenetic study of the *Macaranga* associated *Crematogaster* ants on a molecular basis using mitochondrial DNA sequences. To address the question of possible cospeciation within the *Crematogaster-Macaranga* system the phylogeny of the ant partners is then compared with the phylogeny of their host plants (Blattner et al., 2001; Davies et al. 2001) taking the existing ecological and behavioural data into account.

1.1 Comparison of associations patterns

A crucial moment of the symbiosis is its beginning. A queen of a specific partner ant has to find a host plant suitable for colonization. Successful localization of a host plant and establishment of a colony may be influenced by inter- and intraspecific competition (Longino, 1989; Perlman, 1992; Yu and Davidson, 1997), morphological features (Davidson et al., 1989; Federle et al., 1997; Brouat et al., 2001a), chemical cues (Fiala and Maschwitz, 1990; Inui et al., 2001), or habitat preferences of both partners (Benson, 1985; Davidson et al., 1991; Longino, 1991; Yu and Davidson, 1997) and may lead to specific associations. Most ant-plant symbioses have been studied in detail at this stage of the onset of the association. However, work on temporal variation and dynamics of the associations on

adult trees is sparse, although it is just as vital for both partners in the association to reach the reproductive stage and produce offspring successfully. Secondly, long term field experiments have shown that obligate *Macaranga* myrmecophytes do not survive without the herbivore protection conferred by their specific partner ants (e.g., Fiala et al., 1989, 1994; Heil et al., 1997; Itioka et al., 2000; Heil et al., 2001a). Life-histories of both partners should therefore be at least partly correlated to ensure a stable population of both partners as well as the continuance of the association over several generations.

Turnover of ant species through time on larger plants have been reported from *Acacia* (Janzen, 1975 for South American species; Young et al., 1997 and Palmer et al., 2000 for an African species), *Leonardoxa africana* (McKey, 1984), *Tachigali* (Benson, 1985), and *Maieta* (Vasconcelos, 1990). Changes in species composition with dominance of one species in larger plants have also been found in *Clidemia*, *Tococa* and *Cordia* (Davidson et al., 1989) as well as in *Cecropia obtusifolia* (Longino, 1991). Complete loss of its ant-partner *Cladomyrma maschwitzi* possibly due to loss of ant related traits was reported from *Crypteronia griffithii* (Moog et al., 1998).

Under the presumption of an evolutionary specialisation one would expect that the differences in life-history traits of the host plants have led to different adaptations in the life-histories of ant colonies as well. However, especially in a system where species guilds are interacting and host switches may have occurred mutualists may not be adapted that well and associations may be stable only over a short time window. One focus in this study is therefore the question whether life-histories of both partners in the mutualism are matched. Associations between young and adult trees of different *Macaranga* species were compared and I studied the following questions: (a) Do adult *Macaranga* plants continue to attract ants i.e. provide nesting space and invest in food bodies? (b) Are adult trees still regularly inhabited by ants? –and if so, are these the original primary colonies or do we find a turnover of different colonies over time? And finally (c) do species compositions of associations change?

1.2 Molecular phylogeny of the *Crematogaster* (*Decacrema*) partner ants

The recurring non-random colonization patterns found in the *Crematogaster-Macaranga* associations (Fiala et al., 1999) may be the outcome of two different processes: They are either due to increased host usage by the ants that is followed by cospeciation of the ant partner and its respective host plant species or they may be the outcome of ecological "species sorting" (sensu Jordano, 1987; Davidson et al., 1991). In ecological species sorting repeatable patterns of association are due to biotic and abiotic environmental factors in the absence of evolved specificity. Abiotic factors may be, for instance, coinciding habitat preferences of both ants and plants. A biotic factor would be competition with other arboreal ant species for host plants (Davidson et al., 1991). Evidence for cospeciation by ants and host plants is often hardly distinguishable from ecological species sorting that is due to coinciding habitat preferences of ants and plants.

The molecular phylogeny of the *Decacrema* partner ants provides a useful tool to disentangle the two processes of cospeciation vs. ecological species sorting when it is compared to the phylogeny of the respective host plants (Blattner et al., 2001; Davies et al., 2001), especially together with the existing ecological data. Congruence between phylogenies of interacting lineages would be expected if speciation in one partner (e.g., the host) is accompanied or followed by speciation in the other partner (Clark et al., 2000).

As the two approaches are so different in methodology this thesis is split into two parts. Results obtained with each approach will be discussed directly within the chapter. At the end of the thesis is a synoptic discussion of both approaches.

1.3 Species involved

1.3.1 The plants: *Macaranga*

The palaeotropical plant genus *Macaranga* THOUARS (Euphorbiaceae) comprises approximately 280 species (Whitmore, 1969; Whitmore, 1984; Davies, 2001) with a range stretching from West Africa through Asia, North Australia to the Fiji Islands. The centres of diversity of *Macaranga* are the islands of Borneo and New Guinea (Whitmore 1981) where approximately half of the described species are found.

Most *Macaranga* species are light demanding pioneer plants that naturally grow in secondary forest, along riverbanks or forest gaps. At least in Asia *Macaranga* are mainly found in humid forest, with their centre of distribution being the lowland dipterocarp rainforest areas. Due to human activities potential habitats for these pioneer species have largely increased during the last century and as a consequence *Macaranga* species are now frequently found along roadsides, forest edges and logged areas (Whitmore, 1984; Davies et al. 1998).

A conspicuous feature of many *Macaranga* species is their association with ants that vary from loosely facultative and unspecific to occasionally colonized species, to obligate ant-plants -or myrmecophytes- that are inhabited by specific plant ants (for a review see Fiala, 1996).

Facultative ant-plants of the genus *Macaranga* attract a variety of unspecific arboreal ant species by offering extrafloral nectar or food bodies (Fiala and Maschwitz, 1991).

The obligate myrmecophytic *Macaranga* species offer food in the form of food bodies that are produced by leaves or stipules of the plants (Fiala and Maschwitz, 1992; Fiala, 1996). Host plants provide nesting space in the form of a central cavity inside the trunk and branches that develops through pith degradation, or in some cases has to be excavated by the ants. The host plant species that become hollow by themselves can already be colonized as seedlings by ants when they have reached a height of about 10 cm and have the first swollen internodes (Fiala et al., 1999). Host plant species that have to be actively excavated by the ants are usually colonized a little later from app. 50 to 70 cm height onwards,

possibly due to their smaller stem diameter as a sapling that does not allow colonizing queens to enter the plant. (Fiala et al., 1999; and personal observation).

1.3.2 The ants: *Crematogaster* subgenus *Decacrema*

Natural History

In the beginning of the studies of the association between *Macaranga* and its partner ants it was believed that host plants are inhabited by a single but very variable species only, named *Crematogaster borneensis* André (Baker, 1934; Tho, 1978; Fiala, 1988).

In the meantime it is known that a number of similar species from the subgenus *Decacrema* as well as one *Crematogaster* from a different subgenus (supposedly *Crematogaster* (Itino et al., 2001)) are associated with *Macaranga* as well as several specific species of the genus *Camponotus* (Maschwitz et al., 1996; Federle et al., 1998a and 1998b). The ants from the subgenus *Decacrema* that are the predominant associates of *Macaranga* host plants are easily identifiable by their 10-segmented antennae. However, taxonomy of the *Decacrema* is still obscure (see below).

To date little is known about the process of location and recognition of host plants by colonizing queens. It is likely that chemical cues are involved as queens have to find their host plants in spite of their patchy distribution (Inui et al., 2001). Queens were found to colonize saplings or small *Macaranga* host plants all around the year (Fiala and Maschwitz, 1990; and personal observation). When a colonizing queen finds an unoccupied plant, it sheds her wings and chews an entrance hole into an internode. Colony founding is generally claustral and by a single queen, although frequently more than one colonizing queen is found per sapling. The queen starts laying eggs and after a few weeks, the first workers emerge by reopening the entrance hole or chewing new holes and then start patrolling the plant surface. Aside from herbivores that are deterred workers also keep off competing ants. Each tree is finally dominated by a single colony that presumably stays monogynous.

Endophytic coccids, that are a third specific partner in the associations between *Decacrema* ants and *Macaranga* enter the association only after the emergence of first workers. During their crawler stage the coccids are passively transported onto the surface of host plants by wind drift and then carried into the internodes by workers (Heckroth et al., 1998; Heckroth, 2000). Coccids seem to play a major role in the provisioning of carbohydrate rich food for workers, especially in times where food production of the plant is reduced (Heckroth, 2000).

Nomenclature of the species

The earlier taxonomic literature on *Macaranga* inhabiting *Decacrema* ants is scarce and scattered, containing descriptions (mainly by André, 1896; Forel, 1910 and 1911; Viehmeyer, 1916; see enumeration in Emery, 1921; Chapman and Capco, 1951; or Bolton, 1995) of various species, ”subspecies”, and "varieties" based on only few individuals, mainly workers which are mostly unsuitable for species identification as species can only be identified by queen morphology. The originally described *C. borneensis* alone comprises nine of these ‘forms’.

Earlier therefore eight morphologically distinct morphospecies (msp.) (*C*. msp. 1 to *C*. msp. 7 and *C*. msp. 9) within the subgenus *Decacrema* and one msp. from another subgenus (*C*. msp. 8, that exclusively inhabits *M. winkleri* and presumably belongs to the subgenus *Crematogaster*; Fiala et al., 1999; Itino et al., 2001) that are obligatorily associated with *Macaranga* were recognized (Fiala et al., 1999).The validity of this morphospecies-concept was supported by the constancy of host plant choice of different mspp. over wide geographic ranges as well as a constancy of ecology and life-history traits of each msp.. However, especially in Borneo the association patterns can be very complex as often even several closely related host plant species occur sympatrically.

Three mspp. from the work of Fiala et al. (1999) were synonymized with already described species (see Table 4 in chapter 3.1.1) by comparing the specimens with the holotypes of museum material. *Crematogaster borneensis* André corresponds to *C.* msp. 1 (Fiala et al., 1999), *C.* msp. 4

(Fiala et al., 1999) could be identified as *Crematogaster captiosa* Forel and *C.* msp. 6 (Fiala et al., 1999) could be synonymized with *Crematogaster decamera* Forel. Other mspp. may be new species as no matching type material could be found. The discription of these species is in progress and will be published elsewhere.

Only these taxa were synonymized with holotypes of described species that were collected from the same area as the holotype or showed only little DNA sequence divergence as preliminary molecular data point towards high geographic variability. Taxa that are morphologically and ecologically similar to these holotypes but show strong sequence divergence and might therefore be reproductively isolated are only placed close to these holotypes (cf.).

Whether these molecular differences allow the designation of these varieties as true species with discontinuous character or are only due to geographical variability within species remains to be investigated. Thus, although *Crematogaster borneensis* André matches *C.* msp. 1 morphologically but was sampled in different sites than the holotype, *C.* msp. 1 was only placed near *C. borneensis*. Taxa that cannot be synonymized at all still retain their msp.-number as they may be new species and get an additional geographic designation in the phylogenetic trees (PM= Peninsula Malaysia, NEB= Sabah/ North-East Borneo, NWB= Sarawak/ North-West Borneo, B= Brunei, see Table 4 in Part B: 3.1.1: Collecting sites and studied species).

In a preliminary taxonomic study two species-groups within the subgenus *Decacrema* were identified comprising species with **morphological** similarities: The first group of mspp. (including *C*. cf. *borneensis*, *C*. msp. 2, *C. captiosa*, *C*. msp. 5) have queens that are brown in colour and their eye-length (largest possible length) is at least 1/3 of the head length (measured from the posterior margin of the head to the insertion point of the mandibles). This group will henceforth be called the *captiosa*-group. The second group, containing all other mspp. according to Fiala et al. (1999) (*C*. msp. 3, *C*. *decamera*, *C*. msp. 7 and *C*. msp. 9) have very dark brown or black queens that are smaller in body size compared to queens

from the *captiosa*-group as well as smaller eyes that are less than 1/3 of the head-length. This species group will henceforth be called *decamera*-group. (Note: Results of the molecular phylogeny show that this latter group is separated into two, however, it is homogenous from morphological characteristics as well as life-history traits. For better understanding it will be treated as a homogenous group in the ecological part of the study.)

2 Part A: Comparison of association patterns

2.1 Comparison of association patterns: Methods

2.1.1 Study sites and species studied

The study was conducted in Selangor, Peninsula Malaysia (Ulu Gombak Forest Reserve (UGFR) and the surrounding area) as well as in two parts of Sabah, Borneo (Poring Hot Spring (PHS) and Telupid) during three field trips between March 1999 and November 2000. Plants grew mainly along former logging roads, a few in secondary forest. The study was started in the UGFR and concentrated on the most common *Macaranga* species and their *Crematogaster* (*Decacrema*) partner ants. The *Macaranga* species were all inhabited specifically (> 95 %, Fiala et al., 1999; pers. obs.) by only one partner ant msp. as saplings or small trees (branches of the crown still within reach from the ground). A comparative study was then conducted in PHS with the same associations if possible, to detect local differences in life-history traits of ant colonies. However, as not all *Macaranga* species examined in the UGFR are found in PHS, I studied comparable associations of the same ant msp. on closely related *Macaranga* species (according to the molecular phylogeny of Blattner et al., 2001; and preliminary classification into sections by Whitmore (1975); species identifications also followed Whitmore, 1975 and Davies, 1999 for *M. angulata*).

UGFR: *Macaranga griffithiana*, *M. hypoleuca* (Reichb. f. & Zoll.) Muell. Arg, *M. hosei* King ex. Hook f., *M. bancana* (according to latest revision of Davies, 2001; it was incorrectly referred to as *M. triloba* in the past (e.g. Whitmore 1975)) *M. hullettii* King ex Hook. f..

Sabah: *M. motleyana*, *M. hypoleuca, M. pearsonii* Merr. (as equivalent to *M. hosei*), *M. indistincta* Whitmore (as equivalent to *M. bancana*) and *M. angulata* Davies.

Ants were collected and stored in alcohol. Voucher specimens are kept at the collection of UC Davies, USA with P. Ward.

2.1.2 Association patterns and dynamics of associations

From each tree species specimens ranging in size from saplings to adult trees (trees with the largest dbh found in the forests) were examined for their ant-inhabitation. As colony censuses are not possible in the intact symbiotic systems, trees had to be felled. The trunk as well as the branches were split open longitudinally to gain access to the whole ant colony. By felling trees differing in size I was able to gain insight into colony development. This has to be pieced together from several colonies in a snapshot fashion as observation of a colony over several years that lives mostly inside the trunk and branches without damaging either the colony or the host-plant is impossible. However, by closely examining the associations one can gain information about colony dynamics reaching beyond the current state of the ant colony and host plant.

The trees were also examined for new colony foundings by specific *Crematogaster* ants as well as for unspecific arboreal ants using the nesting space inside the domatia. The number of queens of specific partner ants as well as their position in the trunk were recorded. If more than one queen per colony was found, spermathecae were dissected under a stereomicroscope to check whether all were inseminated.

Colonizing queens usually start founding colonies in the internodes of the stems of small *Macaranga* seedlings which do not yet have any branches. Queens stay in the lower part of the stem during their lifetime. However, queens also colonize bigger trees if there is no other large colony active on the surface. Queens founding a colony on adult trees may either do so at the apex of the main stem or at the tip of each branch as they are not able to bite holes into woody plant tissue (which characterises older branches or stem parts). Therefore queens found in lower parts of the trunk of larger trees were regarded as the original founding queens and queens found inside internodes of side branches as newly colonizing queens. In some *Macaranga* species the pith is not self-degrading but has to be excavated by the ants (e.g., *M. motleyana*, *M. hosei* and *M. pearsonii* of this study). In trees with permanent ant-inhabitation branches and the trunk are completely excavated by the ants, forming a tubelike system running through the whole tree. If trees are not inhabited for some

time the pith is not excavated and hardens so that it cannot be excavated any more. This is an excellent means to ”read” trees: When trees are felled not only their current ant-inhabitants can be examined but the signs of previous ant-inhabitation or periods where no ants inhabited the tree are still visible.

I can only indirectly give an estimation of the age of the trees by growth rates recorded in the literature. Since growth rings are missing in *Macaranga* as in most other trees in the everwet tropics, I have to use measurements of height and diameter (at breast height, dbh) of the trees as indications of age. Primack and Lee (1991) measured growth rates of 23 *Macaranga* species over a period of 15 years, including most of the species examined in this study (except for *M. motleyana, M. angulata* and *M. indistincta*). Mean growth rates of trees in a logged area was at max. about 1.6 cm in dbh per year. This means that trees reaching 10 cm dbh were at least 6 years old but most trees grew slower. As some of the smaller tree species examined in this study hardly ever reach that dbh (e.g. *M. hullettii* growing > 1000 m a.s.l or *M. angulata*) this estimation is suited only for the fast and tall growing species like *M. hosei* and *M. hypoleuca*. Specimens from the latter two species are frequently found with a dbh > 15 cm dbh are frequently found, which should be at least 10 years old when estimated conservatively. Maximum height of trees examined in PHS was in general less than in UGFR as the study site has been logged only 7 years ago. UGFR was logged partly approximately 30 years ago.

2.1.3 Onset of alate production and colony density

Whole small colonies were collected in order to determine the approximate size of the colony where each morphospecies examined starts producing alates. Host plants were cut into pieces and collected in a bag containing chloroform and transferred to the lab. There the number of workers, brood and alates was counted.

To estimate mean colony density of each morphospecies I randomly picked two to three comparable sidebranches from the crown region of

each tree with an approximate length of 1m or above and collected and counted them likewise.

2.2 Comparison of association patterns: Results

2.2.1 Life-history traits of the morphospecies

Onset of alate production

The examination of life-history traits revealed two different groups: all mspp. studied belonging to the *decamera*-group, begin alate production when colonies are still relatively small and have less than 800 workers (*C*. msp. 3, *C*. *decamera* and *C*. msp. 7) whereas all species of the *captiosa*-group that were examined, begin with alate production in bigger colonies containing at least 3000 workers or more (*C*. cf. *borneensis*, *C*. msp. 2 and *C. captiosa*) (see Table 1).

Table 1: Onset of alate production in the different morphospecies. Workers of whole colonies were counted as well as brood (larvae and pupae; eggs omitted). Queenless colonies were omitted in this table. Tree-length is length of stem and branches of the smallest tree containing a colony with alates taken together. If no alates were found then the tree-length of the biggest tree examined is given.

Ant species	**Host plant**	**n**	**No alates (worker + brood)**		**Alates (smallest colony)**				**Tree-length [m]**
			smallest colony	biggest colony	worker + brood	females	males	alate brood	
C. cf. *borneensis*	*M. motleyana*	5	1871+1555	3353+1502	-	-	-	-	7.55
C. msp. 2	*M. hosei*	2	1200+652	3180+3224	-	-	-	-	6.60
C. msp. 3	*M. angulata/ M. indistinta*	12	549+629	977+845	727+637	32	62	32 (female)	2.75
C. captiosa	*M. bancana*	6	2869+2630	3822+3482	5371+3238	44	16	201 (female)	10.7
C. cf. *decamera*	*M. hypoleuca*	11	473+721	615+1335	535+400	1	0	20 (female)	2.25
C. msp. 7	*M. motleyana/ M. angulata*	3	-	-	517+480	10	2	17 (female)	2.45

I also found sexuals in queenless colonies: Two colonies of *C.* msp. 2 on *M. hosei* (1182 workers and 1934 worker respectively, larvae and pupae were found but no eggs) and 1 colony of *C. captiosa* on *M. bancana* (1568 workers and brood). One colony of *C*. msp. 2 had only female brood; the other two colonies contained alates of both sexes. Queenless colonies of *C.* cf*. borneensis* on *M. pearsonii* also usually contained alates of both sexes.

Onset of reproduction in the ant colonies was before their respective host plants reached maturity (personal observation).

Worker density of colonies

Colony density was only checked in UGFR and thus only for the morphospecies found there. *C.* cf*. borneensis* and *C.* cf*. decamera* were both collected from *M. hypoleuca*, *C*. msp. 2 from *M. hosei*, and *C. captiosa* from *M. bancana.* For results see Table 2.

Table 2: Worker density of four different morphospecies: All values are from UGFR only. Each tree that was examined was inhabited and dominated by only one colony. Monogynous and polygynous colonies of *C. captiosa* and *C.* cf. *decamera* were pooled as no significant differences in worker or brood density due to colony structure was found. Workers of *C*. msp. 2 are biggest of all mspp. (unpubl. results).

Ant species	Host plant	n trees	Workers per m	Brood per m
C. cf*. borneensis*	*M. hypoleuca*	12	770 ± 391	321 ± 241
C. msp. 2	*M. hosei*	11	367 ± 137	202 ± 105
C. captiosa	*M. bancana*	18	451 ± 268	296 ± 155
C. cf*. decamera*	*M. hypoleuca*	13	270 ± 86	168 ± 90

Density of workers varied greatly between morphospecies and ranged from on average 270 ± 86 workers per m branch found in *C.* cf. *decamera* to 770 ± 391 workers per m branch found in *C*. cf. *borneensis*. Density of *C.* cf*. borneensis* was equally high when collected from *M. motleyana*

(unpubl. results). Polygynous and monogynous colonies of *C. captiosa* and *C.* cf*. decamera* did not differ significantly in colony density, neither in workers nor in brood.

2.2.2 Temporal variability of the association patterns

Associations between ants of the subgenus *Decacrema* and their *Macaranga* host plants were found to be stable over periods of time, long enough to enable reproduction of the ant colony and (in most cases) the host plants too. All adult trees still provide nesting space as well as food for the ants.

Associations examined in Peninsula Malaysia

Macaranga griffithiana – Crematogaster cf. *borneensis*

M. griffithiana may become 12-20 m high, rarely bigger in primary forest (Whitmore, 1975). Eleven *M. griffithiana* trees between 2.7 m height/ 1.1 cm dbh and 11.2 m height/ 14.6 cm dbh were felled (mean 7.0 ± 3.6 m, median 8.5 m height). Most trees were inhabited by monogynous colonies of *C.* cf*. borneensis*. However, a number of larger trees was also found to be colonized by unspecific arboreal ant species. Only on small trees were queens of *C.* cf*. borneensis* found nesting in the trunk (> 4 m height, n = 5) with one exception in a tree of 8.5 m height / 7 cm dbh, where the queen was also situated in the lower part of the trunk. Bigger trees were all newly colonized by *C.* cf*. borneensis* as indicated by the location of founding queens which were situated in the branches and not in the trunk.

Three of 11 trees were dominated by an unspecific *Crematogaster* sp. (non-*Decacrema*) that had polygynous and polydomous colonies and built carton galleries on the surface of the branches. These ants were observed collecting food bodies and carrying them into the nest inside the domatia, however, they did not provide herbivore protection for the tree and most shoots were damaged by lepidopteran larvae and/ or adults and larvae of curculionid beetles. Although these unspecific *Crematogaster* ants often occupied large parts of the tree they did not prevent *C.* cf*. borneensis*

queens from colony founding in unoccupied branch domatia. We found max. 28 new colony foundings of *C.* cf. *borneensis* per tree, most with brood and some with a small number of workers.

Macaranga hosei – Crematogaster msp. 2

M. hosei may grow up to 32 m (Davies et al., 1998). The 18 *M. hosei* trees felled were between 4.7 m height/ 0.9 cm dbh and 22.2 m height/ 29.6 cm dbh (mean height 17.1 ± 4.7 m, median 17.45 m). Fifteen trees were inhabited by a monogynous colony of *C.* msp.2. In 11 of the 18 trees (61 %) a queen of *C.* msp. 2 was found nesting inside the trunk, in the other trees either one queen of *C*. msp. 2 with a dominating colony or several queens of *C*. msp. 2 with small non-dominating colonies were found in the domatia of branches. New colony foundings of *C*. msp. 2 as well as very rarely of *C*. cf. *borneensis* were found on trees that were inhabited by a weak colony (low worker density) only.

Two trees did not have a dominating colony of *C.* msp. 2: One tree (22.1 m height/ 19.4 cm dbh) was inhabited by one colony of dolichoderine ants as well as several small colonies of *C.* cf. *borneensis* distributed all over the crown region with non-overlapping territories thus non of them dominating the tree. Another tree (21 m height/ 22.4 cm dbh) was inhabited by several colonies of *C.* cf. *borneensis* and *C.* msp. 2, also no colony dominating, with each colony inhabiting several branches and foraging for food bodies on these branches only. Overall on 5 of 18 (36 %) trees unspecific ants (*Camponotus* sp., a small myrmicine and one dolichoderine ant species) were found, none dominating a tree though and not keeping the specific ants from colony founding and foraging.

Macaranga hullettii – Crematogaster msp. 3

On Peninsula Malaysia *C.* msp. 3 is mainly found above an altitude of approximately 900 m a.s.l. in *M. hullettii* –one of the few myrmecophytic *Macaranga* species still found at that elevation.

Nine trees were felled between 1.9 m height/ 1 cm dbh and 12 m height/ 10.2 cm dbh (mean height 5.0 ± 3.2 m, median 3.4 m). *M. hullettii* may grow up to 18 m (Davies et al., 1998) but stays smaller in higher elevations with shorter internodes (Whitmore, 1975; personal observation). All trees were inhabited by a monogynous colony of *C.* msp. 3 and no unspecific ants were found nesting inside the domatia.

Macaranga bancana – Crematogaster captiosa

All 17 *M. bancana* trees that were felled contained colonies of *C. captiosa*. Colonies of *C. captiosa* in *M. bancana* were found to turn secondarily polygynous, containing between 3 to app. 60 inseminated queens. I felled 17 trees from two size classes (8 trees < 10 cm dbh and 9 trees ≥10 cm dbh between 12 m height/ 9.5 cm dbh and 18.8 m height/ 15 cm dbh: *M. bancana* may grow up to 23 m height (Davies et al., 1998; personal observation). Seven of the 9 trees ≥ 10 cm dbh contained a polygynous colony. New colony foundings of *C. captiosa* were found in the crown region of trees that were inhabited by weak original colonies only.

Macaranga hypoleuca – Crematogaster cf. *borneensis* and *Crematogaster* cf. *decamera*

M. hypoleuca may grow up to 24 m (Whitmore, 1975). Fifty specimens of *M. hypoleuca* were examined ranging from the size of a sapling (25 cm height) to fully grown trees of 17.5 m height/ 20 cm dbh (mean height 11.1 ± 4.6 m, median 11.9 m; saplings < 50 cm excluded). The trees were deliberately assigned to 4 size classes (< 5 m; 5 to 10 m; 10 to 15 m and > 15 m in height; see Figure 1). Ant-inhabitation differed significantly between size classes (Craddock-Flood-x^2: $p < 0{,}001$; n=50).

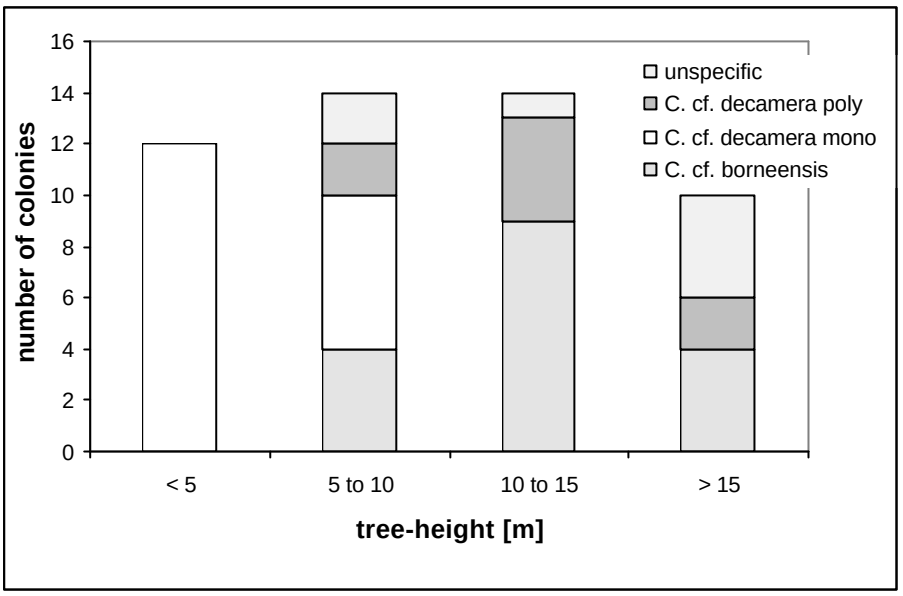

Figure 1: Ant inhabitants on 50 specimens of *M. hypoleuca* examined in UGFR. The ant inhabitation between the different size classes differs significantly (Craddock-Flood-x^2: $p < 0{,}001$; n = 50). (unspecific = trees dominated by a colony of unspecific arboreal ants; poly = polygynous; mono = monogynous)

Saplings and small trees (< 5 m height) were exclusively inhabited by monogynous colonies of *C.* cf. *decamera* (n = 12). In the bigger trees colony structure of *C.* cf. *decamera* as well as the specificity of the association changed (see Figure 1): Trees between 5 and 10 m height contained both monogynous (42.8 %) and secondarily polygynous (14.3 %) colonies of *C.* cf. *decamera* as well as monogynous colonies of *C.* cf. *borneensis* (28.3 %) and unspecific ants (14.3 %) (*Camponotus* sp., *Technomyrmex* sp., *Dolichoderus sp.* and *Crematogaster difformis*). These unspecific ants dominated the trees they were found on. With increasing tree height the percentage of colonies of *C.* cf. *decamera* decreased further (28.6 % on trees 10 to 15 m high and 20 % on trees > 15 m.) and *C.* cf. *borneensis* was found more frequently (64.3 % of colonies on trees between 10 and 15 m height and 40 % on trees > 15 m) as well as more unspecific ants that dominated the host plants (40 % of trees > 15 m were inhabited by unspecific arboreal ant species). On trees > 10 m all investigated colonies of *C.* cf. *decamera* were polygynous (mean dbh of trees with polygynous colonies was 7 cm).

In the crown region of bigger trees only queens of *C.* cf. *borneensis* or of unspecific ants attempted colony founding, no colony foundings of *C.* cf. *decamera* were found. However, this was not due to the presence of unspecific ants since they did not keep the specific *C.* cf. *borneensis* from colony founding in branch domatia.

One tree (17.5 m / 63 cm dbh) was dominated by a colony of *C*. msp. 2. The ants did not show the usual aggressive behaviour towards a biologist cutting down their host plant and the tree had suffered severe herbivore damage as the apices of more than 80 % of the branches were damaged.

Associations examined in Sabah, NE-Borneo

Macaranga motleyana – Crematogaster cf. *borneensis* and *Crematogaster* msp. *7*

Nine trees of *M. motleyana* were examined in Telupid (close to PHS, but at lower elevation and drier) between 0.3 m (the treelet was already dominated by one colony) to 9.2 m height/ 8.8 cm dbh. Smaller trees were inhabited by *C.* msp. 7 whereas all four examined trees > 5 m were inhabited by *C.* cf. *borneensis*. All colonies were monogynous.

Macaranga pearsonii – Crematogaster cf. *borneensis* and *Crematogaster* msp. 2

M. pearsonii is closely related to *M. hosei* (Blattner et al., 2001) but stays smaller, with tree height up to 22 m (Whitmore, 1975). Like in *M. hosei* domatia do not become hollow by themselves via pith degradation but have to be excavated by the ants. I opened 31 saplings with colony foundings only when plants were not yet dominated by one colony. In addition 40 trees between 2.6 m height/ 1.6 cm dbh and 15.2 m height/ 13 cm dbh (mean height 5.2 ± 2.8 m, median 4.3 m) were examined. Saplings were colonized by two species: *C.* cf. *borneensis* (25.6 %) and *C*. msp. 2 (74.4 %) and often housed more than one founding colony (one or several queens with brood per domatium).

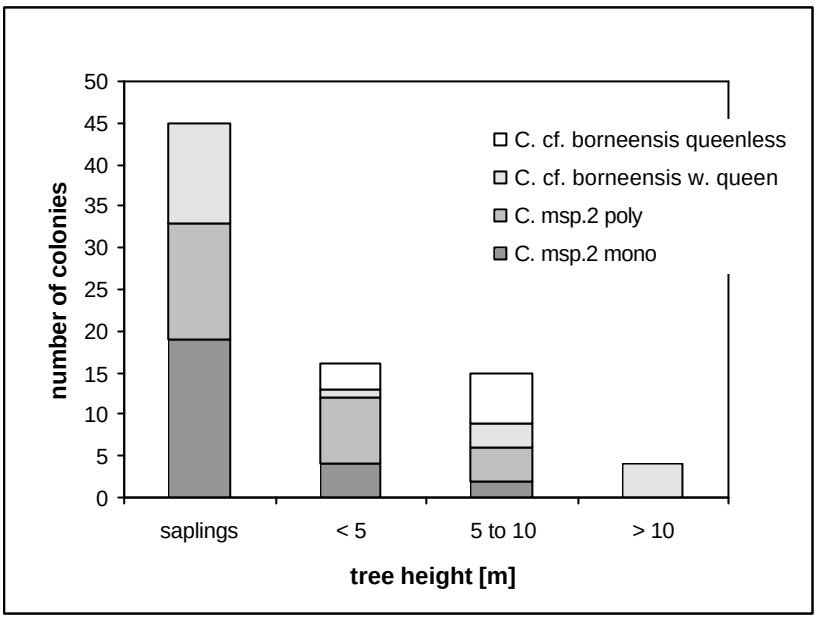

Figure 2: Ant inhabitants of *M. pearsonii* examined in PHS. Plants that only housed incipient colonies were all counted as saplings. All others plants that were examined contained established colonies. (poly = polygynous colonies; mono = monogynous colonies). Colonies of *C.* cf. *borneensis* often did not contain a queen (”queenless”).

In this association I observed a shift in the pattern of the association with increasing tree height from *C.* msp. 2 to *C*. cf. *borneensis* (see Figure 2). Although more colony foundings of *C*. msp. 2 were discovered on saplings the frequency of established colonies of this *C.* msp. decreased on bigger trees, and none were found on trees > 10 m (n = 4). In the small to medium sized trees (< 5 m height and 5 to 10 m height) colonies of *C.* cf. *borneensis* often contained no queen. (75 % -or 18.7 % overall- of colonies of *C*. cf. *borneensis* in trees < 5 m and 67 % -or 37.5 % overall- on trees between 5 and 10 m). Eggs were not observed in these cases, but the queenless colonies contained alates of both sexes.

Macaranga indistincta* – *Crematogaster* cf. *borneensis*, *Crematogaster* msp. 3 *and Crematogaster captiosa

M. indistincta is reported to grow up to 9 m (Whitmore, 1975). I observed trees of comparable size to *M. bancana* though, growing up to 14 m.

Fourteen specimens of *M. indistincta* were examined from 1.7 m height/ 0.9 cm dbh to 13.6 m height/ 11.4 cm dbh (mean height 5.0 ± 3.6 m, median 2.9 m). Two of these trees were inhabited by *C. captiosa* (2.8 m height/ 1.3 cm dbh and 7.1 m height/ 4.1 cm dbh), all others by *C*. msp. 3. All colonies were monogynous. Additionally new colony foundings of *C*. cf. *borneensis* were observed, but no tree was found being dominated by a colony of this species

On one tree (12.6 m height/ 11.4 cm dbh) a queenless colony of *C*. msp. 3 inhabited the trunk with only few workers left and no brood. In the tips of the branches in this tree I discovered 21 new colony foundings (some still in the claustral stage, some with up to 50 workers) of *C.* cf. *borneensis*. No colony founding of a different msp. was discovered in the crown region. Specificity of the association thus would have changed from *C*. msp. 3 to *C.* cf. *borneensis* within several weeks. Trees of approximately this size or bigger are frequently found to be inhabited by *C.* cf. *borneensis* (Fiala et al., 1999; personal observation).

Macaranga angulata* – *Crematogaster* msp. 3 and *Crematogaster captiosa* and *Crematogaster msp. 7

M. angulata Davies is a small shade-tolerant tree that grows up to 8 m (Davies, 1999). Like *M. indistincta* it is colonized by several specific partner ants regularly. This tree species is not very common and in PHS I found only one big tree of this species.

Eight *M. angulata* trees were examined from 1.6 m height/ 0.7 cm dbh to 8 m height/ 8 cm dbh (mean height 3.1 ± 2.0 m, median 2.4 m). Four trees housed colonies of *C. captiosa* and four were inhabited by *C.* msp. 7.

Compared to former results (Fiala, unpubl.) the percentage of *C. captiosa* found on *M. angulata* is higher in this study. On saplings and host plants found at higher elevations (app. 600 to 900 m a.s.l.) app. two thirds were inhabited by *C*. msp. 3 and only one third by *C. captiosa* (Fiala et al.,

1999; in results then still named *M. depressa*, species was revised and name changed to *M. angulata* by Davies, 1999).

Macaranga hypoleuca* – *Crematogaster* cf. *decamera

Nineteen *M. hypoleuca* trees were examined between 1.9 m height/ 0.9 cm dbh and 11.4 m height/ 12.4 cm dbh (mean height 5.4 ± 3.7 m, median 3.1 m). Except for three trees all were inhabited by colonies of *C*. cf. *decamera* (84 %). One small tree (3.5 m height/ 1.75 cm dbh) that was found on a higher elevation (app. 700 m a.s.l.) was inhabited by *C.* msp. 7; two trees were inhabited by *C.* cf. *borneensis*: one small tree (3 m height/ 1.6 cm dbh) contained a queenless colony as well as one adult tree (11.4 m height/ 12.4 cm dbh) with a queenright colony. I did not find any new colony foundings in the branches and therefore cannot tell which msp. would enter the tree next: again *C.* cf. *decamera* or *C.* cf. *borneensis*.

In contrast to Peninsula Malaysia no polygynous colonies of *C.* cf. *decamera* were so far found in Sabah.

2.2.3 Changes in social structure of colonies

Secondary polygyny

Secondary polygyny in *Crematogaster captiosa*

In young *M. bancana* trees the queen of a monogynous colony is most often surrounded by a lump of eggs and becomes increasingly physogastric as the colony grows. Above the queen the trunk as well as the branches are more or less filled with brood and workers. In monogynous colonies I never found alate females with full spermathecae within the mother-colony (n alates dissected = 213). All 17 trees of the two size classes that were felled for this study were inhabited by *C. captiosa*.

Table 3: Colony composition in 17 *M. bancana* trees. N worker and brood (larvae and pupae) is given per meter. Alates (m=male, f=female) were not counted.

# Tree	Height [m]	d.b.h. [cm]	n queens	Queen-location [m] above ground	n brood per m	n workers per m	Alates
1	12.6	7.6	1	1.7	220-262	687-955	m/f
2	11.6	8.6	1	2.5	145-555	595-697	m/f
3	11.5	8.9	1	0.6	367-420	333-595	m/f
4	11.5	8.9	1	2	432-527	738-766	m/f
5	12.2	9.2	1	1.5	67-481	428-638	m/f
6	12	9.5	1	6	287-525	436-662	m/f
7	13.3	9.9	1	4.1	108-408	254-410	m/f
8	15.2	10	17	3.6 to 10.1	36-437	27-91	m/f?
9	16	10.5	54	-	34-37	257-332	m/f?
10	15	11.1	11	3.1 to 3.8	127-693	535-719	m/f
11	14.4	11.5	22	1.7 to 3.5	629-822	676-800	m/f
12	13.7	11.7	1	2	334-359	112-187	m/f
13	13.4	12.4	3	1.4 to 2.2	447-610	560-651	m/f?
14	12.7	12.7	1	2	8-45	17-55	m/f
15	14	14	64	1.1 to 8.4	105-219	4-162	m/-
16	18.8	15	60	-	433-435	147-435	m/-
17	16.6	15.3	5	10 to 10.6	238-609	699-1097	m/f

All colonies on the trees in this study contained alates and all but two had alates from both sexes (Table 3, tree #15 and 16). The alate females were usually found in the trunk and only seldom in the branches whereas most of the males were found inside the branches.

In seven of the eight trees with a dbh. < 10 cm, just as in the smaller trees, I found only one strongly physogastric queen per colony in the lower part of the trunk. In one colony, however, that contained no physogastric queen, I found 17 young queens in the trunk. None of these queens was as strongly physogastric as the single queens in the other colonies that

were examined. Dissection of the spermatheca showed that all but one of these queens were inseminated, although five were still alate with intact wings. They were distributed between 3.6 m and 10.1 m (see Table 3 and Figure 3) above the ground in the tree trunk, with 5 wingless queens at different heights being surrounded by a clump of eggs (between 50 and 250 eggs).

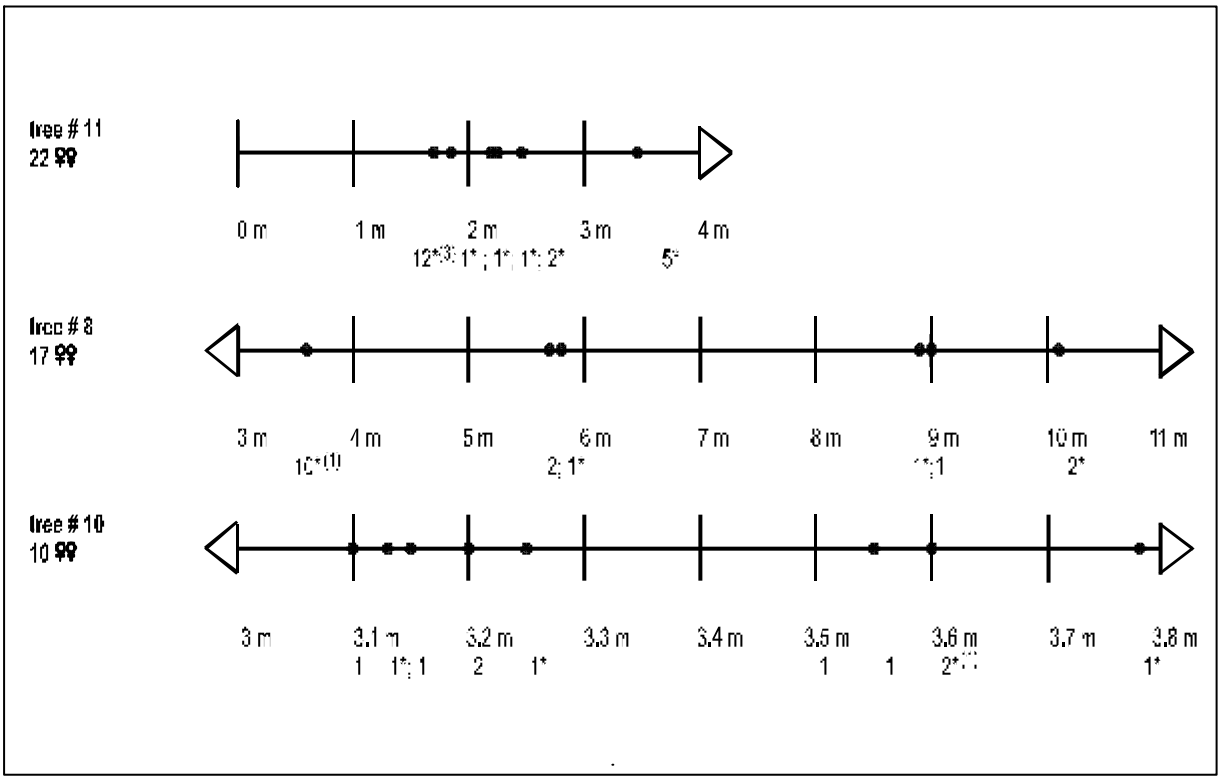

Figure 3: Distribution of inseminated queens in the tree trunk of three selected trees. Each internode containing queens is marked with a dot on the meter–scale. The number of queens found per internode is shown underneath the height (m). The * indicates that eggs were found with each queen in the internode, or, if not all were laying eggs in the internode, the number of egg-laying queens is given in the small brackets behind the *.

In the group of the larger trees with a d.b.h. >10 cm we found more than one queen (between 3 and 64) in the trunk in seven out of nine trees. In one colony with three queens (Table 3, tree #13) all three were surrounded by eggs and were strongly physogastric. In the other polygynous colonies there were no physogastric queens. Although all were inseminated, the development of the ovaries was not equal in all

queens. Only about a third had ovaries that filled the whole gaster. In colonies with more than one queen not all had shed their wings completely. About a third of the queens had between one to two thirds of the wings bitten off, thus preventing them from flying away. When queens were kept inside a box, darkened with red plastic foil (and containing no plant parts) I observed that workers as well as other alates sometimes bit off the distal parts of the wings. On tree #15, which was not as densely populated as most of the other *M. bancana* and had 64 inseminated queens in the trunk, I found 17 other queens of *C. captiosa* in the crown region that all had tried colony foundation independently in separate internodes. They were all still in the claustral stage, some with brood. The colony structure differed significantly with the size (i.e. age) of *M. bancana* (X^2 4.76: $p < 0.05$, trees with d.b.h. < 10 cm versus trees with d.b.h. > 10 cm). Colonies in trees with a d.b.h. < 10 cm usually had one queen only whereas colonies in larger trees became polygynous.

Secondary polygyny in *Crematogaster* cf. *decamera*

Polygynous colonies of *C*. cf. *decamera* contained between 4 and 22 queens that had either no wings or only wing remnants left, similar to queens in polygynous colonies of *C. captiosa*. They were always found close to each other within the connected internodes of the trunk and thus situated within the same domatium, usually within a range of 30 to 60 cm. Dissection of spermathecae showed that all were inseminated and most seemed to be active egg-layers as they had developed yellow bodies and were surrounded by a clump of eggs. Queens showed no aggression towards each other. If a polygynous colony contained alate females in the branch domatia, their spermathecae were dissected as well but – like in *C. captiosa* on *M. bancana*– were never inseminated. The density of workers as well as brood (larvae and pupae) of monogynous and polygynous colonies of *C*. cf. *decamera* (likewise *C. captiosa*) did not differ (Mann-Whitney U-Test, two tailed, $p = 0.66$ for workers and $p = 0.83$ for brood respectively ($n = 13$)). Polygynous colonies contained 297 ± 108 workers /

167 ± 99 brood, and monogynous colonies contained 253 ± 72 workers / 169 ± 91 brood per m branch length.

Secondarily polygynous colonies in this species were not a local phenomenon on Peninsula Malaysia as they also occurred at another study site (Bukit Rengit) that is separated from UGFR by the central mountain range .

Pleometrotic colony founding

A very conspicuous result of the examination of *M. pearsonii* and its association with *Decacrema* ants (in PHS) was that 42.4 % of the colony foundings of *C.* msp. 2 were pleometrotic. Queens varied slightly in colour and size and female alates from other colonies were accepted when placed into founding associations when. These colonies of *C.* msp. 2 obviously stayed polygynous, since I also found established colonies that dominated the trees containing several thousand workers which still had several queens.

The relative number of polygynous established colonies of *C.* msp. 2 was twice as high compared to established monogynous colonies. Number of queens of *C.* msp. 2 varied between 2 and 7 in pleometrotic colony foundings as well as in established polygynous colonies. However, the mean number of queens of pleometrotic colony foundings was significantly lower than in established polygynous colonies (average 2.6 queens in pleometrotic foundings (n = 14) and 4.2 in established polygynous colonies (n = 12); Mann-Whitney U-Test, $p < 0.001$).

2.3 Comparison of association patterns: Discussion

This study revealed a dynamic pattern of temporal variation and distribution of ant associates in the genus *Macaranga* (see Figure 4 for overview). Local variation in ant associates has been documented in a few other ant-plant systems (e.g., Ward, 1993; Davidson and McKey, 1993b; Longino, 1989; Yu and Davidson, 1997) but determinants of this variability

in species composition remain largely unknown. Only very little information exists beyond the beginning of the associations -colony founding and establishment of a colony that monopolizes the host tree. I tried to follow the patterns and temporal variation of different associations of the *Crematogaster-Macaranga* ant-plant system from establishment of the colonies in saplings to adult trees and compared the life-histories of the specific partner ants in reference to their host-trees. This study shows that the ant-plant symbiosis was in general maintained also on larger trees but I found a succession of specific partner ants in some of the associations as well as variation in colony structure among the different mspp..

Like on saplings, an asymmetry in dependence (Fonseca and Ganade, 1996) also exists between the partners of mature associations.

2.3.1 Dynamics of the associations over time

No change in the ant inhabitation pattern

On four host-plant species (*M. hosei*, *M. hullettii*, *M. bancana,* and *M. angulata*) original colonies seemed to be very durable as the queen was usually found inside the trunk indicating that this might still be the initial founding queen. Such a parallel life-cycle of ant colony and host plant should be positive for the plant side as the plants benefit from constant herbivore protection by the ants. It can be accomplished by different strategies of the ants: (a) by a monogynous colony where the initial founding queen has a life-span as long as that of its host tree (which I regard as very probable, at least in some cases); (b) by prolonging the life-span of the initial colony via secondary polygyny (*M. bancana – C. captiosa* (Feldhaar et al., 2000) and *C.* cf*. decamera* on *M. hypoleuca*) or (c) by possible replacement and turnover of single egg-laying queens within the colony (for that I have no indication but I cannot entirely rule it out).

Change in the pattern of ant inhabitation

In several associations the pattern of ant inhabitation changed regularly and I found an ontogenetic succession of different specific partner ants of the subgenus *Decacrema*. Depending on the msp. of the initial colony, either a change to another ant partner occurred (often from a msp. of the *decamera*-group towards *C.* cf*. borneensis,* belonging to the *captiosa*-group) or -which might often be undetected- a succession of several colonies of the same msp.. On *M. hypoleuca* (UGFR) I found *C.* cf*. decamera* only on small trees whereas bigger trees were mostly inhabited by unspecific arboreal ants or by *C.* cf*. borneensis*. In PHS I did not find *M. hypoleuca* that were big enough to be really comparable but the results suggest that *C.* cf*. borneensis* eventually replaces *C.* cf*. decamera*. In three further species (*M. pearsonii*, *M. indistincta* and *M. motleyana*) the specificity of the association shifted from a majority of an original colonizing msp. (*C*. msp. 2, *C*. msp. 3 and *C*. msp. 7, respectively) on treelets to *C.* cf*. borneensis* on bigger trees. On *M. griffithiana* (UGFR) *C.* cf. *borneensis* was found on small as well as on big trees but a considerable percentage of unspecific arboreal ants had been able to enter the association and I found indications for high colony turnover in this msp., like a high number of queenless colonies and numerous new colony foundings in branches.

Specific partner ants as well as unspecific arboreal ants may only enter larger host plants and succeed in colony founding and establishing a new colony when a tree is no longer inhabited at all or by a weak colony only. The plant surface is then no longer patrolled by workers and thus herbivores as well as potential founding queens are not driven off. The host plant may be left without partner ants if the initial colony does not have a lifespan as long as that of its host plant (Fonseca, 1993; Fonseca and Benson, 1995) or if the initial colony is actively evicted and eventually replaced by superior competitors (e.g., Davidson et al., 1989; Young et al., 1997; Palmer et al., 2000). Active eviction of a colony could not be observed on *Macaranga*, but cannot be ruled out. Aggression between specific partner ants was only observed among incipient colonies for dominance of the host plant.

I observed differences in colonisation patterns and colony life spans between mspp. that facilitate the ontogenetic succession of specific partner ant species. In comparison with mspp. of the *captiosa*-group the mspp. of the *decamera*-group have smaller queens and workers, short lived colonies with relatively low worker density, they start producing alates earlier (partly unpubl. results). Morphospecies of the *decamera*-group colonize saplings only whereas mspp. of the *captiosa*-group are able to colonize branches of larger trees as well. Founding queens of mspp. from the *decamera*-group were never found > 5 m above ground whereas those of the *captiosa*-group were discovered even 20 m above ground. As a result any host plant that has lost its initial colony will only be recolonized by quens of mspp. from the *captiosa*-group or opportunistic unspecific ants. The differences in colonizing behaviour may be due either to differences in searching behaviour or to physical constraints of the ants. For the rather small queens of mspp. from the *decamera*-group it may be easier to colonise saplings that have fewer woody elements than the harder branches of trees. This tendency towards later colonization by mspp. of the *captiosa*-group (*C. captiosa* is an exception as it also colonizes small saplings) may also be favoured by habitat and plant characteristics. *M. griffithiana* that is mostly colonized by *C.* cf *borneensis* is often found in swampy areas where queens may avoid flooding of the nest by later colonization. Ontogenetic differences in stem diameter make some host plant species earlier accessible for colonization by foundresses than others (Fiala and Maschwitz, 1992). Especially host plant species where domatia have to be actively excavated by the workers have smaller stem diameters as small saplings (e.g. *M. motleyana*, *M. griffithiana*, *M. hosei* and *M. pearsonii*, personal observation).

Food resources produced by the plant may also play a role in colonization patterns as well as for colony-growth as only treelets or bigger trees in productive habitats may be able to sustain a large or fast-growing colony (see also Davidson et al., 1991; Davidson and Fisher, 1991; Davidson and McKey, 1993b; Palmer et al., 2000). Morphospecies of the *decamera*-group often colonize host plants in less productive habitats like higher elevations or small shaded forest gaps. In these habitats foundresses of

mspp. of the *captiosa*-group are rarely found. For *Decacrema* colonies there are indications that food resources rather than nesting space (Fonseca, 1999) are the limiting factor for colony populations. Heil et al. (2001b) could show that colony density and size of colonies of *C. captiosa* was correlated with food supply rather than amount of nesting space on *M. bancana*. Although collected from the same host plant (*M. hypoleuca*) worker density of *C.* cf. *borneensis* was on average about threefold higher than that of *C.* cf. *decamera*. Maximum size of colonies and worker density are thus partly depending on environmental circumstances like energy resources but are also liable to life-history traits of each msp. as these results demonstrate.

Ontogenetic change of ant inhabitants inevitably occurs when foundresses of both groups compete for host plants with a long lifespan due to their differences in searching behaviour. Foundresses of the *decamera*-group colonize saplings earlier but colonies are relatively short-lived and abandon the trees. Host plants are then re-colonized by foundresses from mspp. of the *captiosa*-group only. This change in ant inhabitants is crucial to the host plant as it suffers higher herbivore damage due to lower worker density during the time when this change occurs (Gaume et al., 1997; Palmer et al., 2000) or it may even become dominated by unspecific arboreal ants. Unspecific ants do not protect the host plant against herbivores and may be regarded as parasites in the mutualism. They usually only use the nesting space and rarely the food resources of the plant (personal observation) but may prevent the specific partner ants from establishing a colony or at least prolong the time before the tree has an intact specific colony again. I did not find a regular parasite on *Macaranga* host-plants, like *Cataulacus mckeyi* on *Leonardoxa africana*, that regularly occurs on approximately one fourth of all trees (Gaume and McKey, 1999). However, there are some indications that the protective benefit of different specific ant partners on their respective *Macaranga* host species may vary (Federle, 1998; Itioka et al., 2000; Fiala, unpublished results).

The high fecundity, high queen mortality and high colony turnover in comparison to other *Decacrema* species point towards a different ecological strategy (Yu and Wilson, 2001) of *C.* cf. *borneensis* compared

to other msp. of the *captiosa*-group that have very stable colonies, e.g. *C*. msp. 2 on *M. hosei*. *C.* cf. *borneensis* is rather a generalist in colony founding as it colonizes a wider scope of *Macaranga* host plant species than all other mspp. and may also colonize abandoned trees in the crown region. However, due to the high colony turnover host plants colonized by this msp. are more often rendered without ant defence during their lifespan and thus face higher herbivore damage compared to host plants that are colonized by other msp. and greater risks of being parasitized by unspecific ants. Comparative studies of different specific ant partners on the same host plant species are still lacking.

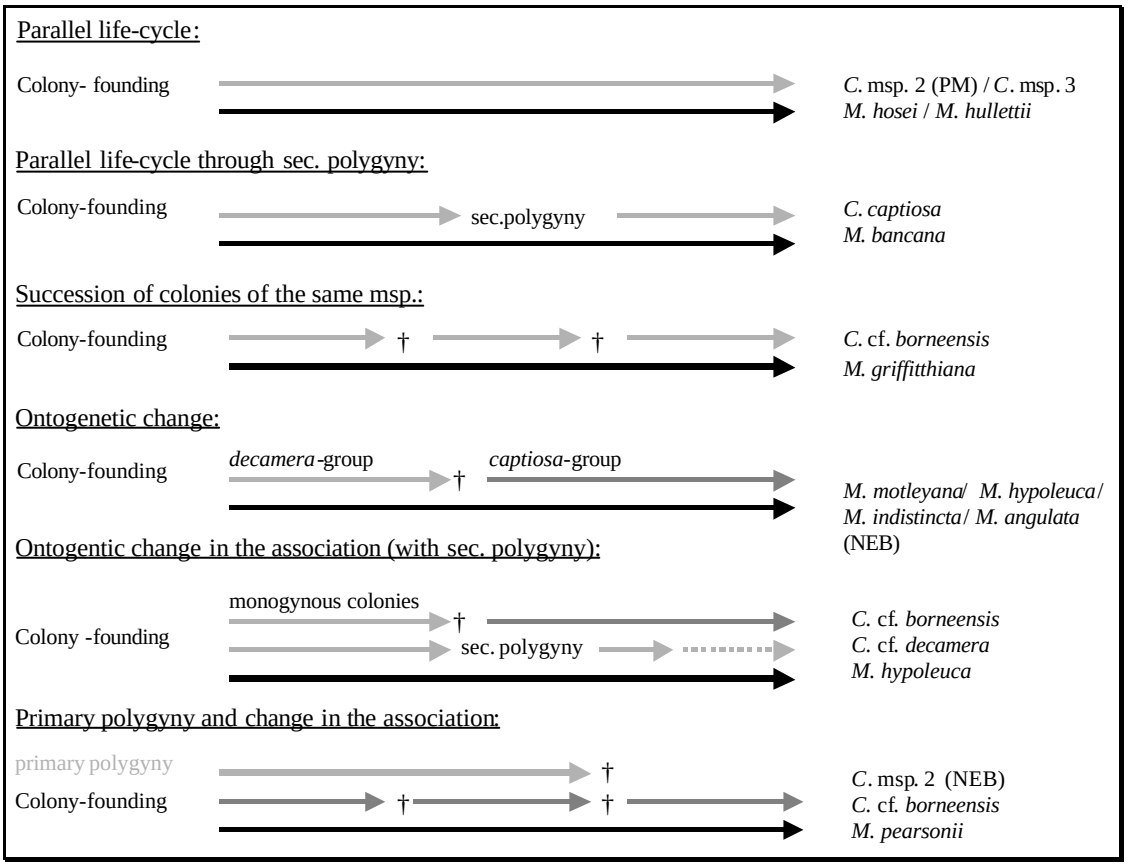

Figure 4: Overview of the different patterns of temporal variation found in the associations between *Macaranga* and *Decacrema* ants from colony founding to the death of the host-plant or ant-colonies. Black arrows: life-span of host plants; grey arrows: life-span of ant colonies; †: death of colonies; dotted arrow: some colonies of *C.* cf. *decamera* are found on trees of the biggest size class but most colonies perish in spite of secondary polygyny. PM = Peninsula Malaysia, NEB = North-East Borneo.

2.3.2 Changes in colony structure

Secondary polygyny in Crematogaster captiosa and Crematogaster cf. decamera

In *C. captiosa* and *C.* cf. *decamera* I found a change in colony structure in mature colonies (Feldhaar et al., 2000) as they turned secondarily polygynous. This was a local phenomenon as I could only detect secondarily polygynous colonies on Peninsula Malaysia but not in PHS. The data suggest that the change in colony structure occurs in a similar way in these two mspp.

I assume that the colonies turn polygynous only after the death of the original foundress as I have never found a strongly physogastric queen together with the other still non-physogastric queens in the trunk of the host trees. Presumably a number of alates are inseminated and several, though not all of them, start laying eggs. During that time the number of workers as well as brood is reduced (personal observation). The number of queens in the polygynous colonies is again reduced in an unknown way. The remaining queens are all strongly physogastric (at least in *C. captiosa*; queens of *C.* cf. *decamera* never become as physogastric) and egg-laying, which indicates that they coexist at least for a period of several weeks or maybe even months.

Secondary polygyny enables the ant colonies to prolong their lifespan, even after the death of the original founding queen and make use of the resources of the host tree continuously. In the association *M. bancana-C. captiosa* a parallel life-cycle and a stable mutualism that is not invaded by unspecific arboreal ants is attained via secondary polygyny of the ant colony (see Figure 4). Therefore the association would be expected to end because of the natural death of the tree as a secondarily polygynous colony is potentially immortal if queens are replaced. However, secondarily polygynous colonies of *C.* cf. *decamera* still vanish from their *M. hypoleuca* hosts without any signs of competition or fighting and the relative number of colonies decreases on adult trees. One possible explanation could be that the female alates stay inside the mother colony (Feldhaar et al., 2000) and are also mated by males from the mother

colony. Due to the sex determination system based on heterozygosity, inbreeding would lead to a high number of diploid males that are homozygous at the sex locus and are costly to colonies as they are sterile and slow colony growth (Crozier and Page, 1985; Strassmann, 2001). Wing remnants on the thorax of some of the young queens point towards the possibility that no mating flight took place as wings are usually shed wholly before entering a host plant (Feldhaar et al., 2000).

Compared to other plant-ants *C. captiosa* and *C.* cf. *decamera* show an unusual type of secondary polygyny. In contrast to these two *Crematogaster* species usually the number of queens increases continuously as new queens -often daughter queens- are adopted into the colony as it grows (Janzen, 1973; McKey, 1984; Fonseca, 1993). The adoption of queens begins in an early stage of the colonies when they still have only few workers. In colonies of *Petalomyrmex phylax* on *Leonardoxa africana* a ratio of 1 queen per 200 worker was found (McKey, 1984). In *C. captiosa* and *C.* cf. *decamera* however, daughter queens are not constantly readopted as polygynous colonies are only found at a later stage where the colonies have > 10000 workers (personal observation) and the number of queens does not increase.

Pleometrosis in Crematogaster msp. 2

Pleometrotic colony foundings of *C*. msp. 2 were unexpected since this has not been found in system before. There are two interesting aspects: First, colonies of *C*. msp. 2 from PHS had been collected for the past seven years but polygynous foundings have never been found before (Fiala, personal communication and personal observation). From the year 1999 onwards the majority of colony foundings was pleometric and queens in founding associations presumably unrelated. Such a transition from haplometrotic to pleometrotic colony founding has been reported for a few other plant ant species when density of established colonies increases and number of nesting sites is limited (Davidson et al., 1991; Vasconcelos, 1993). In contrast to most other ant species -not only plant associated- with pleometrotic colony founding (for a review see

Bernasconi and Strassmann, 1999) the colonies of *C*. msp. 2 stay polygynous and fighting or aggression between queens was so far not observed. This behaviour is very rare in general and reported for very few ant species only (e.g. Mintzer, 1987; Trunzer et al., 1998).

The number of queens did not decrease after eclosion of the first workers, on the contrary, I found an increase in mean queen number in established colonies compared to colony foundings instead. This may be due to two reasons: Either additional queens have been adopted by the colonies after eclosion of the first workers or colonies of foundress associations containing more queens have a higher survival rate and a higher rate of establishing a colony. I consider the second possibility as the more likely. The results show that foundress associations have a higher survival rate and are more successful in establishing colonies than single queens of *C*. msp. 2. Secondly pleometrotic colonies may produce the first workers earlier than haplometrotic ones as well as a larger number of workers and thus have an advantage in the attempt to gain dominance of a sapling when it is colonized by multiple incipient colonies (e.g. Verhaagh, 1994; Sommer and Hölldobler, 1995; Choe and Perlman, 1997). Competition for nesting space is high as we found more than one founding colony on most saplings. *M. pearsonii* is also one of the rare cases where direct interspecific competition occurs frequently as saplings are colonized by foundresses of *C.* cf. *borneensis* as well as *C*. msp. 2. If resource competition is lower between founding queens monogyny will be favoured as each individual queen then has a better chance of reproducing (McKey et al., 1999).

Polygyny, regardless of whether it is primary or secondary, may be a plastic response to resource availability or competition (Janzen, 1973; Longino, 1989; Davidson and McKey, 1993b; Herbers, 1993).

3 Part B: Molecular phylogeny of the ants of the subgenus *Decacrema*

3.1 Molecular phylogeny of the ants of the subgenus *Decacrema*: Methods

3.1.1 Collecting sites and studied species

Ant samples were obtained from Peninsula Malaysia (PM): Ulu Gombak Forest Reserve (UGFR), Genting Highlands and Kuantan as well as several sites in North Borneo: In Sabah (NEB): Poring Hot Spring (PHS), Bukit Taviu and Telupid; in Sarawak (NWB): Mulu area and Lambir area; in Brunei: Labi road. Some mspp. do not occur in all regions (e.g. *C*. msp. 7 and *C*. msp. 9 are endemic to Borneo or the central eastern part of the Malay Peninsula, respectively). Specimens were collected alive and subsequently stored in 98 % ethanol. Voucher specimens are kept at Würzburg and the collection of UC Davies, (USA) with P. Ward.

As outgroups I used one *Crematogaster* species belonging to the subgenus *Crematogaster* that lives in obligate symbiosis with *Macaranga winkleri* (Fiala et al., 1999: *C.* msp. 8) and another undescribed arboreal *Crematogaster* from a different subgenus, that is associated with the epiphytic *Dischidia nummularia* (Asclepidiaceae) found on the giant bamboo *Gigantochloa scortechinii* (*Crematogaster* sp. 1, Kaufmann et al., 2001).

Table 4: (see next page)

List of specimens used in the molecular phylogeny. Sequences were submitted to EMBL-GenBank. Host-plants and collecting localities of the investigated species. Collecting sites: PM= Peninsula Malaysia; NEB= Sabah, North-East Borneo, NWB= Sarawak, North-West Borneo; B= Brunei. When species were synonymized their former morphospecies-number is given in the second column.

Species	Morpho-species	Host-plant	Collecting site	COI - GenBank Accession No.	COII - GenBank Accession No.
Crematogaster sp. 1		epiphyte	Gombak, PM	AF 499933	AF 499968
C. (*Crematogaster*) msp. 8		*M. winkleri*	PHS, NEB	AF 499934	AF 499969
C. cf. *decamera* #51	msp. 6	*M. hypoleuca*	Gombak, PM	AF 499935	AF 499970
C. cf. *decamera* #52	msp. 6	*M. hypoleuca*	Gombak, PM	AF 499936	AF 499971
C. cf. *decamera* #57	msp. 6	*M. hypoleuca*	PHS, NEB	AF 499937	AF 499972
C. cf. *decamera* #120	msp. 6	*M. hypoleuca*	PHS, NEB	AF 499938	AF 499973
C. cf. *decamera* #121	msp. 6	*M. hypoleuca*	PHS, NEB	AF 499939	AF 499974
C. decamera #125	msp. 6	*M. hypoleuca*	Mulu, NWB	AF 499940	AF 499975
C. (*Decacrema*) msp3 #46		*M. hullettii*	Genting, PM	AF 499941	AF 499976
C. (*Decacrema*) msp3 #106		*M. hullettii*	Genting, PM	AF 499942	AF 499977
C. (*Decacrema*) msp3 #114		*M. motleyana*	PHS, NEB	AF 499943	AF 499978
C. (*Decacrema*) msp3 #115		*M. motleyana*	PHS, NEB	AF 499944	AF 499979
C. (*Decacrema*) msp3 #136		*M. umbrosa*	Mulu, NWB	AF 499945	AF 499980
C. (*Decacrema*) msp3 #137		*M. umbrosa*	Mulu, NWB	AF 499946	AF 499981
C. cf. *borneensis* #42	msp. 1	*M. griffithiana*	Rawang, PM	AF 499947	AF 499982
C. cf. *borneensis* #104	msp. 1	*M. hypoleuca*	Gombak, PM	AF 499948	AF 499983
C. (*Decacrema*) msp2 #44		*M. hosei*	Gombak, PM	AF 499949	AF 499984
C. (*Decacrema*) msp2 #55		*M. pearsonii*	PHS, NEB	AF 499950	AF 499985
C. (*Decacrema*) msp2 #61		*M. pearsonii*	PHS, NEB	AF 499951	AF 499986
C. (*Decacrema*) msp2 #130		*M. hosei*	Mulu, NWB	AF 499952	AF 499987
C. cf. *borneensis* #54	msp. 1	*M. indistincta*	B. Taviu, NEB	AF 499953	AF 499988
C. cf. *borneensis* #111	msp. 1	*M. pearsonii*	PHS, NEB	AF 499954	AF 499989
C. captiosa #48	msp. 4	*M. bancana*	Gombak, PM	AF 499955	AF 499990
C. captiosa #49	msp. 4	*M. bancana*	Gombak, PM	AF 499956	AF 499991
C. captiosa #107	msp. 4	*M. bancana*	Kuantan, PM	AF 499957	AF 499992
C. captiosa #116	msp. 4	*M. indistincta*	PHS, NEB	AF 499958	AF 499993
C. captiosa #117	msp. 4	*M. angulata*	PHS, NEB	AF 499959	AF 499994
C. captiosa #131	msp. 4	*M. umbrosa*	Lambir, NWB	AF 499960	AF 499995
C. (*Decacrema*) msp. 5 #50		*M. hypoleuca*	Maran, PM	AF 499961	AF 499996
C. (*Decacrema*) msp. 5 #108		*M. hypoleuca*	Maran, PM	AF 499962	AF 499997
C. (*Decacrema*) msp. 5 #132		*M. lamellata*	Labi Road, B	AF 499963	AF 499998
C. (*Decacrema*) msp. 7 #59		*M. motleyana*	Telupid, NEB	AF 499964	AF 499999
C. (*Decacrema*) msp. 7 #58		*M. motleyana*	Telupid, NEB	AF 499965	AF 500000
C. (*Decacrema*) msp. 9 #53		*M. hypoleuca*	Maran, PM	AF 499966	AF 500001
C. (*Decacrema*) msp. 9 #26		*M. hypoleuca*	Maran, PM	AF 499967	AF 500002

3.1.2 DNA-Isolation

Prior to DNA extraction, the gaster of each specimen was removed because it contains an unidentified substance inhibiting the polymerase chain reaction. The head and alitrunk of specimens were ground in liquid nitrogen. DNA samples contained either one queen or five workers or five larvae from the same colony. A classical phenol/ chloroform extraction protocol was used for DNA isolation:

Ants that were stored in ethanol were dried for 10 min prior to DNA isolation. Specimen were homogenized in 100 µl extraction buffer A (containing 10 mM Tris-HCl pH 7.5, 60 mM NaCl, 10mM EDTA, 0.15 mM spermine, 0.15 mM spermidine). Then 100 µl buffer B (containing 0.2 mM Tris-HCl pH 9.0, 30 mM EDTA, 2 % SDS) as well as 5 µl of proteinase K (12.5 mg/ ml) were added and the homogenate incubated at 37° C for 60 min.

DNA was extracted once with 200 µl phenol and once with 200 µl chloroform-isoamylalcohol (25:1). After adding 1/10 volume 3 M sodium acetate solution the DNA was precipitated from aqueous phase with two volumes of 100 % ethanol overnight. The DNA was dried and resuspended in low TE. The quality and amount of DNA was checked with minigels (Sambrook et al., 1989).

3.1.3 PCR-Methods

For a subset of 7 specimens 1309 bp of mitochondrial DNA were sequenced to verify the gene order and the position of the noncoding region. These sequences contained partial cytochrome oxidase I and II (COI and COII), the $tRNA^{leu}$ (67 bp) and a noncoding region (197 bp) between the end of COI and the $tRNA^{leu}$. For amplification primers C1-J-2195 (alias COI-RLR) and CO2-Croz. (modified C2-N-3661; the first 3`base is deleted) (Crozier and Crozier, 1993; Simon et al., 1994) as well as two internal primers (IPF 5` >GAT TTA TTC A(CT)T GAT T(CT)C C< 3` and IPR 5`>AGT TCA AT(AT) AGA TT(AG) CCA TG< 3`) were used.

For the phylogenetic analysis only partial COI (483 nucleotides, corresponding to positions 784 to 1267 of *Apis mellifera* mtDNA (Crozier

and Crozier, 1993)) and partial COII (439 nucleotides, corresponding to positions 3677 to 4116 of *Apis mellifera* mtDNA) sequences were used.

Amplification profile for C1-J-2195/CO2Croz. was 95°C for 3 min, 30x (94° C for 1 min, 45° C for 1 min, 72° C for 1.5 min), 72° C for 5 min. PCR-reaction mix for 25 µl contained 1.5 U Taq DNA polymerase (native, without BSA, MBI Fermentas), 2.5 µl standard 10X buffer (MBI Fermentas), 2.0 µl of 25 mM $MgCl_2$ (final concentration of 2 mM, MBI Fermentas), 0.3 µl 2mM dNTPs (MBI Fermentas) and 0.8 µM of each primer (produced by Carl Roth GmbH, Germany).

For the internal primers (IPF/IPR) the following touchdown profile was used: 94° C for 4 min, 94° C for 40 sec, 50° C for 40 sec down to 45° C for 40 sec with 0.5° C lower in each cycle (12 cycles), 72° C for 40 sec, 25X (94° C for 40 sec, 45° C for 40 sec, 72° C for 40 sec). PCR-reaction mix contained 0.75 U Taq DNA polymerase, 2.5 µl of standard 10X buffer, 2.5 µl of 25 mM $MgCl_2$ (final concentration of 2.5 mM), 0.2 µl 2mM dNTPs and 0.4 µM of each primer (all contents of reaction-mix obtained from the same sources as above).

PCR products were purified by ethanol precipitation in the presence of 4 M NH_4Ac. The precipitated DNA was washed twice with 70 % ethanol. DNA was recovered in 30 µl HPLC purified H_2O.

All PCR-reactions were carried out using a Biometra T1 Thermocycler.

3.1.4 Sequencing

Purified PCR products including the sequencing primers were sent to a sequencing facility (Sequence Laboratories Göttingen GmbH) and directly sequenced by cycle sequencing with Big Dye.

Sequences of partial COI and partial COII were deposited in the EMBLGenBank under Accession-Numbers AF 499933 to AF 499967 for COI and AF 499968 to 500002 for COII.

3.1.5 Phylogenetic Analysis

All DNA sequences could be unambiguously aligned by eye. Base frequencies, variation, and divergence values were determined with PAUP 4.0b10 (Swofford, 2002). Phylogenetic congruence between COI and COII was confirmed with the partition homogeneity test included in the programme.

For the study of the phylogenetic relationships I used several different methods that comprise different approaches towards the given data.

Neighbor Joining Analysis

The Neighbor-Joining method is a phenetic method that quantifies the similarity between the taxa that are examined. Like in other methods based on distance only, there is no distinction of plesiomorph and apomorph characters, but all characters are assumed to be neutral. A tree obtained by Neighbor-Joining algorithm hierarchically joins taxa to groups according to their overall similarity.

A Neighbor-Joining analysis of all 35 taxa was performed with PAUP 4.0b10 using uncorrected p-distances.

Maximum Parsimony Analysis

In general, phylogenies obtained using the Maximum Parsimony criterion yield the shortest possible tree meaning, the number of evolutionary steps needed to explain the given dataset is kept at a minimum (Swofford et al., 1996). Maximum Parsimony

Phylogenies obtained under Maximum Parsimony criterion (using PAUP 4.0b10; Swofford, 2002) were obtained by branch and bound search modus yielding the shortest possible tree. As branch and bound modus would have been too time consuming heuristic search modus was used for bootstrapping in order to determine the strength of support for individual nodes. For all trees characters were all equally weighted. Downweighting of third codon position (weighting scheme: 1st codon position: 1.1; 2nd

codon position: 1.1; third codon position: 1.0) yielded trees of the same length and topology, therefore results are not shown.

Phylogenies for two different datasets were inferred: one including all taxa examined and the second with a subset of all specimens collected in Peninsula Malaysia only. As the ecological study was mostly done in Peninsula Malaysia it was important to evaluate the validity of the morphospecies concept especially for this region.

Maximum Likelihood Analysis

Maximum Likelihood methods incorporate models of evolutionary change, e.g. models for DNA substitution. Under the Maximum Likelihood criterion a history with a higher probability of giving rise to the current state of affairs is a preferable hypothesis to one with a lower probability of reaching the observed state. (Swofford et al., 1996).

Maximum Likelihood analyses (using PAUP 4.0b10; Swofford, 2002) were run with a limited dataset only (omitting all double sequences that had less than 3 bp difference between each other) with different settings to obtain trees comparable to the results of the Bayesian analysis.

Phylogenetic analysis with the following settings were conducted:

1. **No among site variation**, meaning that all sites may only change at equal rates. These settings correspond to the F81 model (Felsenstein, 1981).
2. **Transition- and transversion ratio may be unequal**, with the ratio being estimated from the given dataset. This model corresponds to the HKY85 model (Hasegawa et al., 1985).

Bayesian Analysis

Bayesian analysis of the data was performed with MrBayes 2.01 (Huelsenbeck, 2000; Huelsenbeck et al., 2001) as bootstrapping with Maximum Likelihood methods would have been too time consuming. However, phylogenies obtained under different Maximum Likelihood

settings (see above) matched the topology of the phylogeny obtained with Bayesian analysis.

For Bayesian analysis a smaller dataset of only 27 taxa was used (all doublets were omitted, i.e. taxa of one msp. from the same geographic region with less than 2 bp differences). The best model of DNA substitution for our data set was selected by Modeltest 3.0 (Posada and Crandall, 1998). For the Bayesian analysis I thus used a GTR-model with site-specific rates (GTR + SSR).

Bayesian analysis is based on the posterior probability of a phylogenetic tree and can be interpreted as the probability that the tree inferred from the data is correct. The posterior probability of a tree is approximated with the Markov Chain Monte Carlo algorithm (MCMC) that involves two steps: 1. new trees are proposed by stochastically perturbing a current tree and then either accepting or rejecting it due to its probability. 2. The frequency with which each tree is sampled indicates its probability: trees with higher posterior probability are sampled more often than trees with lower posterior probability.

In the MCMC process we ran four chains (one heated, three cold) simultaneously for 1.000.000 generations with trees being sampled every 100th generation resulting in 10.000 trees. The first 300 trees were discarded because ML scores had not yet reached a stable level (the so called burnin phase). Thus, the posterior probability of the Bayesian phylogeny was determined from 9700 trees. A consensus tree (50 % majority-rule) of these trees was computed in PAUP 4.0b10 (Swofford, 2002). Support values on branches are equivalent to the percentage of trees that contained this node.

3.2 Molecular phylogeny of the ants of the subgenus *Decacrema*: Results

3.2.1 General remarks on the DNA-sequences

Compared to the mitochondrial genome of *Apis mellifera* the gene order of the COI/ COII region differs in the subgenus *Decacrema* as well as other

Formicidae (Wetterer et al., 1998). In ants the gene order is COI/ non-coding region/ $tRNA^{Leu}$/ COII whereas in *A. mellifera* genes are ordered in the following way: COI/ $tRNA^{Leu}$/ non-coding region/ COII (Crozier and Crozier, 1993). The non-coding region shows no length differences in the subgenus *Decacrema* although this region has been shown to be variable in length on genus-level in ants (Wetterer et al., 1998).

Like in most insects (Crozier and Crozier, 1993) is the base composition of the COI/ COII genes of *Crematogaster* (*Decacrema*) strongly AT-biased (69.8 %, see Table 5). There was variation in base composition between codon positions (see Table 5). First and second codon position were less AT biased (64.6 % and 67.9 % respectively) than the third codon position (74.3 %). This is similar to *A. mellifera* (Crozier and Crozier, 1993) and other ants (Brady et al., 2000).

Table 5: Nucleotide composition of the COI/ COII sequences, averaged across all *Crematogaster* taxa, including outgroup taxa (*Crematogaster* sp. and *C. (Crematogaster)* msp. 8):

	% A	**% C**	**% G**	**% T**
All sites (922sites)	30.7	20.9	10.2	38.2
Partial COI only (483 sites)	30.4	20.4	12.7	36.5
Partial COII only (439 sites)	31.0	21.8	7.6	39.6
First codon positions (308 sites)	36.3	17.2	18.2	28.3
Second codon positions (307 sites)	22.2	21.2	10.9	45.7
Third codon positions (307 sites)	33.6	24.2	1.5	40.7

Note: Composition was not statistically different across taxa: all sites: $X^2 = 25.9$, df= 102, P = 1; first pos.: $X^2 = 11.4$, df = 102, P = 1.0; second position: $X^2 = 5.1$, df = 102, P = 1.0; third position: $X^2 = 106.9$, df = 102, P = 0.351; COI vs. COII: $X^2 = 18.3$, df = 102, P = 1.0.

COI and COII were combined in the phylogenetic analysis as partition homogeneity testing showed no significant conflict in phylogenetic signal (P = 0.46) of the two genes (Cunningham, 1997). Of the 922 bases used for the phylogenetic analysis (484 of COI and 439 of COII) 355 were variable. 267 of these sites were parsimony informative (over all taxa).

Third codon positions contained most of the informative sites (209 of 267 or 78.2 %) but did not show saturation within the subgenus *Decacrema* (Figure 5). The combined dataset contained significant phylogenetic information as the skew (g_1) value was significantly below critical value at the $P < 0.01$ level ($P = -0.4992$) (Hillis and Huelsenbeck, 1992).

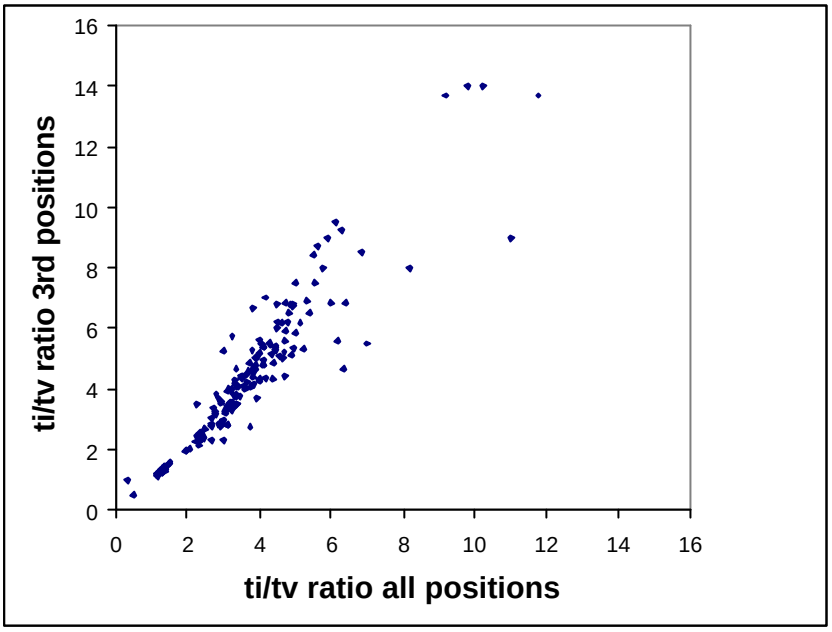

Figure 5: Correlation of third codon position transition/ transversion (ti/ tv)ratio between all species pairs relative to overall transition/transversion ratio. Third codon positions do not show saturation transition/ transversion ratio does not reach a plateau.

The greatest sequence divergence observed within the ingroup was 16.7 %. Maximal observed sequence divergence between in- and outgroup amounted to 20.6 %.

3.2.2 Neighbor-Joining Analysis

The phenogram obtained by Neighbor-Joining analysis based on uncorrected p-distances yielded the same results as phylogenies inferred from cladistic methods (Maximum Parsimony) and Likelihood methods (Maximum Likelihood and Bayesian analysis).

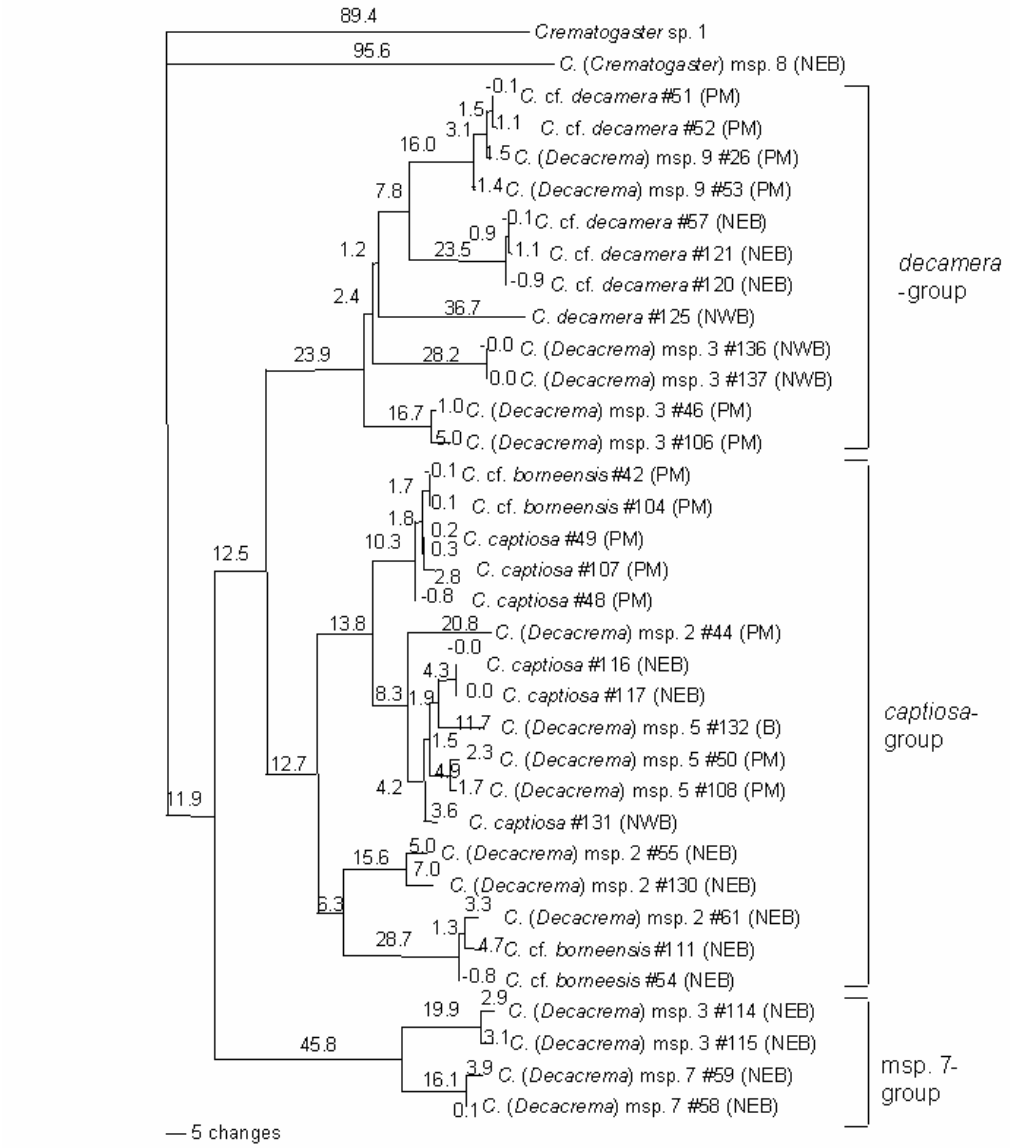

Figure 6: Neighbor-Joining phenogram of uncorrected p-distances of all 33 *Decacrema* taxa and two outgroup species. Distances (similarity of taxa) are given above branch length. Collecting localities given in brackets: PM= Peninsula Malaysia, B= Brunei, NWB= North-West Borneo, NEB= North-East Borneo.

3.2.3 Maximum Parsimony Analysis

The unweighted MP of all 35 taxa (33 *Decacrema* plus 2 outgroup taxa) resulted in twenty most-parsimonious trees with a length of 786 steps (CI = 0.590, RI = 0.830) (Figure 7).

All species of the subgenus *Decacrema* form a monophyletic clade. This clade can be separated into three species groups: the *captiosa*-group, the *decamera*-group and one other group containing two species that are morphologically and ecologically similar to the *decamera*-group but are genetically quite distinct (*C*. msp. 3 var. PHS and *C.* msp. 7, both from NE-Borneo). This latter group will henceforth be called msp. 7-group.

As most of the former work on ecology and biology of the ants has been conducted in Peninsula Malaysia we produced a separate MP analysis of mspp. collected from Peninsula Malaysia only (Figure 8), to evaluate the usefulness of our morphospecies-concept for this region. The unweighted MP analysis resulted in a single most parsimonious tree (length: 446 steps, CI = 0.805, RI = 0.86, 126 characters were parsimony informative). The mspp. were all well separated from each other, except for *C.* cf. *borneensis* and *C. captiosa* that showed only low bootstrap support (Figure 8).

Sequences from conspecific specimens from the same geographic region were identical or differed by up to 6 nucleotide positions only and thus produced unresolved polytomies in the bootstrap analysis (Figure 6 and Figure 7). Specimens from the same msp. and different geographic regions showed much greater differences in most cases and show well supported division into two or three groups respectively that may be considered as isolated subpopulations or cryptic species.

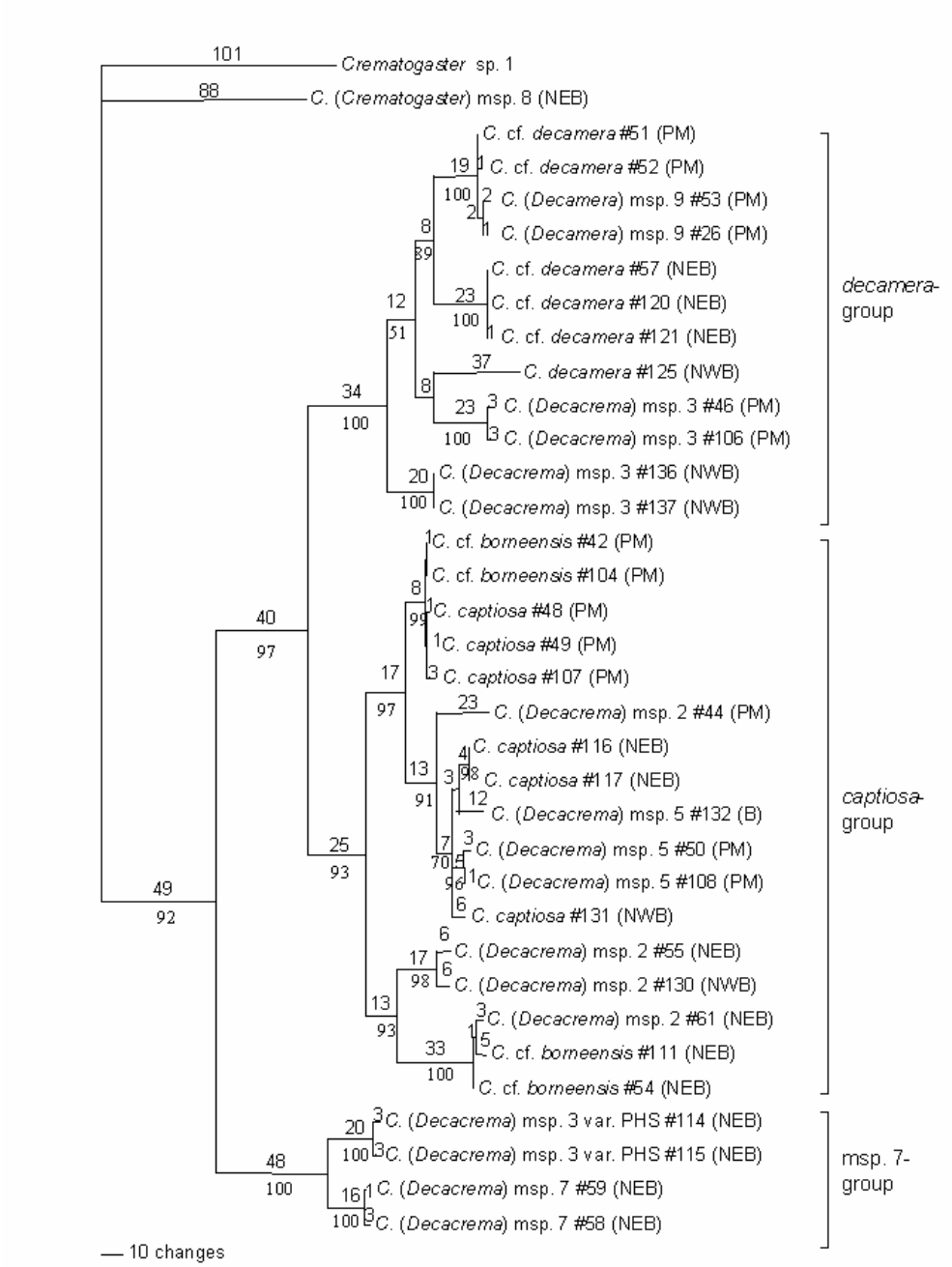

Figure 7: Strict consensus tree of 20 most parsimonious trees (tree length: 786 steps; CI: 0.59; RI: 0.83) obtained by branch and bound search with characters all equally weighted (PAUP 4.0b10, Swofford 2002) of all taxa from different geographic regions (collecting localities given in brackets: PM= Peninsula Malaysia, B= Brunei, NWB= North-West Borneo, NEB= North-East Borneo). Branch-lengths are given above and bootstrap values of 500 replicates of heuristic search below branches. Only bootstrap values > 50 % are shown.

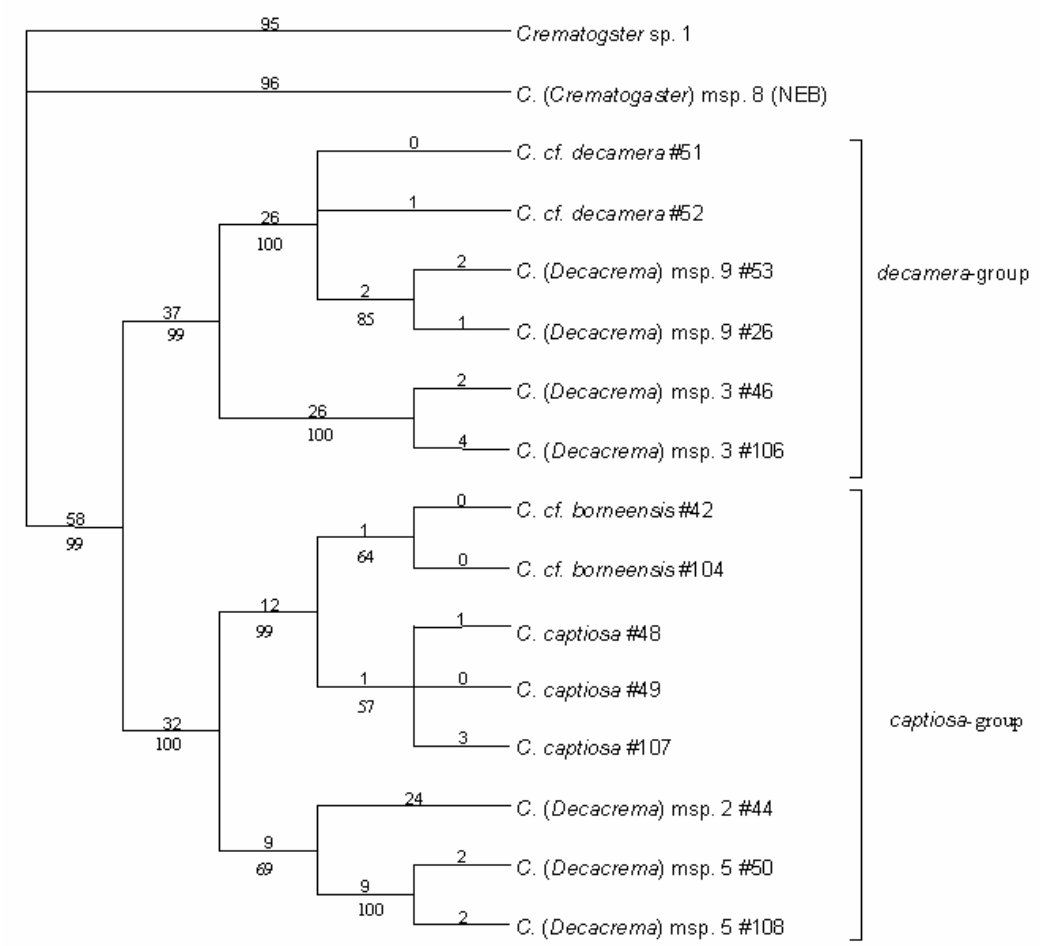

Figure 8: Single unweighted most parsimonious tree (tree length: 446 steps; CI: 0.805; RI: 0.860) with branch-lengths obtained by branch and bound search with characters all equally weighted (with PAUP 4.0b10, Swofford 2002) of taxa collected on Peninsula Malaysia only.

3.2.4 Maximum Likelihood Analysis

Under the Maximum Likelihood criterion two phylogenies were obtained with different settings, i.e. different models of DNA substitution. The phylogeny obtained with the simpler of the two models -the F81 model- that only allows equal rates of substitution at all sites yielded a phylogeny with a lower likelihood score than the one obtained with settings corresponding to the HKY85 model that allows transitions and transversions to occur at different rates (with F81 settings: -lnL = 5332.3 compared to -lnL = 5049.15 with HKY85 settings). The estimated transition-transversion ratio under the HKY85 model estimated from the dataset is 2.848 (see Figure 9 for tree obtained under HKY85 model). Topologies of both trees were similar to the topologies of the trees obtained under different criteria as well as to the Bayesian analysis.

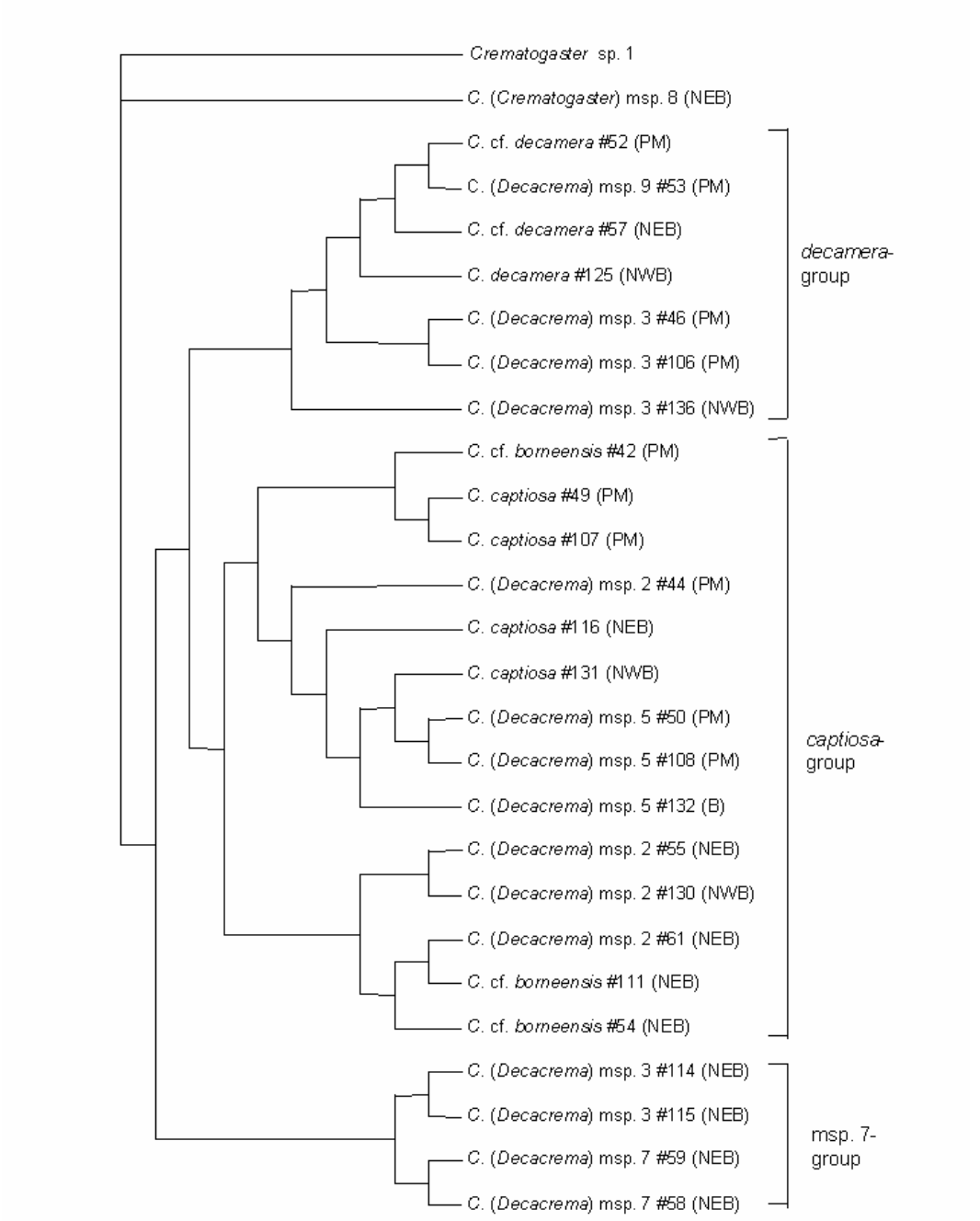

Figure 9: Phylogeny obtained from Maximum Likelihood analysis in heuristic search modus. Likleihood score: -lnL = 5049.15. Likelihood settings corresponding to the HKY85-model. The transition-transversion ratio (2.848) was estimated from the dataset.

3.2.5 Bayesian Analysis

Bayesian analysis with site-specific rates yielded a consensus tree (9700 trees; 50 % majority rule) with the same topology as the tree obtained from MP analysis (see Figure 10: tree description: -ln likelihood = 4378.19; substitution rates for codon positions: 1^{st}: 0.125; 2^{nd}: 0.381, 3^{rd}: 2.291). Generally, Bayesian probabilities and bootstrap values in MP analysis appear to be correlated. Nodes of our tree supported by high bootstrap values in the MP analysis also showed high probabilities in Bayesian analysis. Branches with significant bootstrap support (> 70 %, Hillis and Bull, 1993) are identical in both analyses, with the support values being higher in the tree with Bayesian probabilities, a result that has been found in other phylogenies too (e.g., 70 % bootstrap corresponded to approximately 80 % Bayesian branch support; Whittingham et al., 2002).

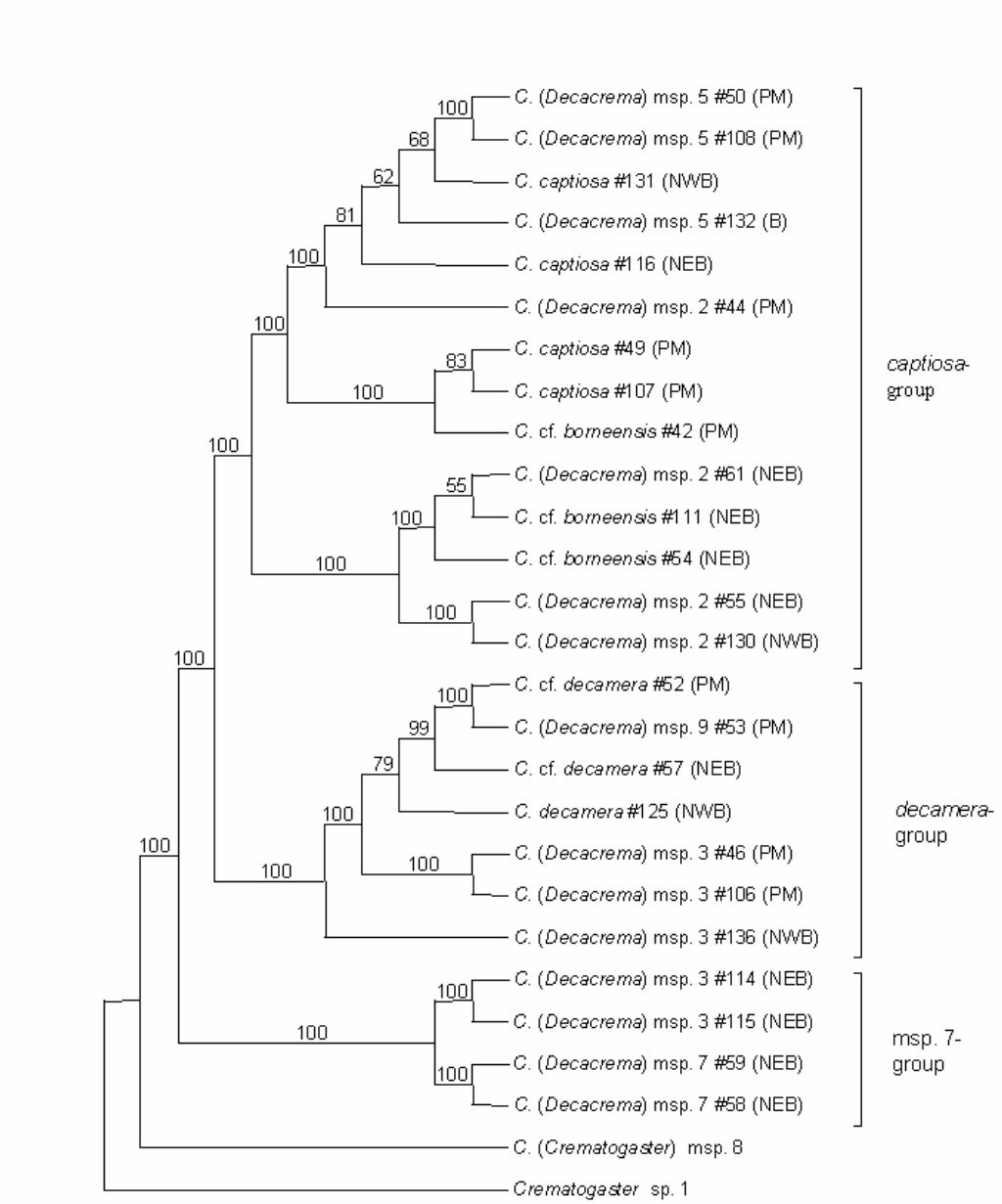

Figure 10: 50 %- majority rule consensus tree of 9700 trees from Bayesian analysis of 27 taxa (doublets omitted) with a GTR–model with site-specific rates (1 million generations, with a tree being sampled every 100th generation; 300 trees discarded as burnin) computed with PAUP 4.0b10 (Swofford, 2002). Mean -ln likelihood = 4378.19. Substitution rates for codon positions were as follows: 1st: 0.125; 2nd: 0.381, 3rd: 2.291.

3.3 Molecular phylogeny of the ants of the subgenus *Decacrema*: Discussion

3.3.1 General remarks

In general, COI and COII are well suited for phylogenetic reconstruction of *Macaranga*-inhabiting *Crematogaster* ants of the subgenus *Decacrema*. The trees obtained are well resolved down to morphospecies (msp.) level and Neighbor-Joining, Maximum Parsimony, Maximum Likelihood and Bayesian analyses yielded trees with identical topologies (Figures 6 to 10). In comparison to the two outgroup species all *Decacrema* species form a monophyletic clade with high bootstrap support (Figures 6 to 10), indicating a single colonization event of the *Macaranga* host plants by the subgenus *Decacrema* followed by subsequent diversification.

The subgenus *Decacrema* is split into three species-groups (*captiosa*-, *decamera*- and msp. 7-group) that are consistent with morphological and ecological features: Species from the *captiosa*-group are morphologically and ecologically quite distinct (e.g., size and colour of queens, colonizing behaviour) from the other two species groups. In contrast members of the *decamera*- and msp. 7-group are quite similar in respect of their morphology and ecology but were clearly separated in our phylogeny. The tree topology (Figures 6, 7, 9, and 10) suggests that the msp. 7- and *decamera*-group represent the basal groups. Then small, dark queens and -in comparison to the *captiosa*-group- smaller and shorter-lived colonies that start reproduction earlier (Feldhaar et al., 2002; Feldhaar unpubl. results) would be the ancestral character states.

3.3.2 Evaluation of the morphospecies concept

One objective of this study was to evaluate our morphospecies-concept (Fiala et al., 1999) as a taxonomic revision of the subgenus is still lacking. The mspp. show a constancy in choice of host plants and are found on the same or, in the majority of cases, closely related host plant species over a wide geographic range (Fiala et al., 1999). As most of our ecological studies of the subgenus *Decacrema* were conducted on Peninsula

Malaysia (PM) it was especially important to see whether the morphospecies-concept is valid for this region.

Samples collected from all mspp. occurring on PM (six of the eight *Decacrema* species) clearly separated into two groups: the *captiosa*- and *decamera*-group (Figure 8). The *captiosa*-group split into 4 taxa that are equivalent to our formerly used mspp. *C.* cf*. borneensis* (*C*. msp 1), *C*. msp. 2, *C. captiosa* (*C*. msp. 4), and *C*. msp. 5, respectively (Figure 8). The *decamera*-group was also separated into three taxa that are also in accordance with the three other mspp. formerly proposed for PM: *C*. msp. 3, *C.* cf. *decamera* (*C*. msp. 6), and *C*. msp. 9, respectively. Only the separation of *C*. cf. *borneensis* and *C. captiosa* was supported by relatively low bootstrap values. Although, *C*. cf*. borneensis* and *C. captiosa* are morphologically close, they differ considerably in their ecology, e.g., choice of host plants. I propose that the lack of genetic divergence between these two species is due to a relatively recent speciation event. This interpretation is further supported by the finding that the *captiosa*-group seems to be the most derived and youngest species group of the subgenus *Decamera*.

When samples from the all sampled populations were analyzed (Figure 6 and 7) considerable geographic variability within mspp. was detected. On this wider geographic range our mspp. are often not clearly separated or rather mspp. are sometimes nested within each other, especially within the more derived *captiosa*-group. It seems that on a wider geographical range some mspp. are a mixture of multiple genetically quite distinct taxa. Whether their morphological similarity is due to convergent evolution remains open for further investigation.

All specimens from each msp. from the same geographic region clustered together, except for one sample from a population of *C.* msp. 2 from NE-Borneo with an unusual form of colony founding (pleometrosis = multiple queens find a colony together) that clustered with *C.* cf*. borneenis* from the same region.

Magnitude of sequence divergence between mspp. occurring in all sampling sites varies strongly. Except for *C. captiosa* where highest value of sequence divergence was 3.8 % between specimens from different

geographic regions I would thus propose that we are dealing with species-complexes rather than a single diverse species. Within these species-complexes ants are hard to distinguish morphologically and also have the same host-plant spectrum. In other phylogenetic studies of attine ants as well as the ants of the genus *Camponotus* using the same mtDNA region approximately the same magnitude of sequence divergence as that found in *C.* msp. 3 separated species or even genera (Wetterer et al., 1998; Brady et al., 2000). In *Camponotus* intraspecific sequence divergence was between 0 % and 3 % and sequence divergence between different subgenera approximately 20 % (Brady et al., 2000).

However, divergence in molecular data and morphology is not always parallel. Although p-distance between *C.* cf. *decamera* (PM) and *C. decamera* (NWB) was high (69 nucleotide substitutions or 7.6 % sequence divergence) queen morphology between both species is very similar. This is even more pronounced in *C*. msp. 3. This msp. is clearly separated into at least three different taxa (Figure 7): It shows more variability in queen morphology than the other msp. and hitherto supposedly comprised two ecotypes, a lowland (NWB) and a highland form (PM) (Fiala et al., 1999). Host plant-spectrum of *C*. msp. 3 differs among the sites due to only localized occurrence of the species.

In contrast in the *decamera*-group *C*. msp. 9 is nested within specimens of *C. decamera* and *C.* cf. *decamera* of different geographic regions. *C*. msp. 9 is endemic to the central parts of Peninsula Malaysia and found on the same host plant species as *C.* cf. *decamera* (PM) (on *Macaranga hypoleuca*). Although, it is only separated from *C.* cf. *decamera* (PM) by 4 nucleotide substitutions (0.3 % sequence divergence) in the COI/ COII region it is morphologically clearly distinct (confirmed by J. Longino, pers. communication), i.e. queens are smaller and differ significantly in their allometry compared to queens of *C. cf. decamera* (PM).

3.3.3 Possible mechanisms of speciation in *Decacrema* ants

Diversification in *Decacrema* ants may be due to several reasons: a) allopatric speciation due to geographic isolation by barriers like

mountain ranges (e.g. the Crocker Range that largely separates the populations of NW- and NE-Borneo and the S-China Sea separating Peninsula Malaysia from Borneo) or b) sympatric speciation due to specialization towards different host plant species. Spreading of the ants is strongly connected to the spreading of their respective host plants as the ants are not able to survive without their plant partners. Thus diversification of the host plants has to be taken into account too.

The first (non-myrmecophytic) *Macaranga* -as pioneer of open places- was hypothesized to originate in the oligocene or early miocene (38 to 15 my ago) when climate was predominantly seasonal and dry (Slik and van Welzen, 2001). Rainforest, the habitat of all myrmecophytic *Macaranga* species, colonized the region in the mid-miocene when the climate changed to perhumid (Morley, 2000), so we assume a development of the first close *Macaranga*-ant associations not before this period. With the advent of quarterny glaciations repeated fragmentation of rainforest sites occurred, leading to isolation and possible further speciation events. Myrmecophytic species, especially in the section *Pachystemon* share very close phylogenetic relationships. This points toward a rather recent rapid radiation of this section. The relatively small amount of molecular and morphological differentiation strongly contrasts with the remarkable diversity of life history characters, exemplified by multiple ecophysiological traits (Davies et al., 2001).

Although *Decacrema* species have diversified after the colonization event of *Macaranga* the groups within the subgenus cannot be mapped onto the phylogeny of their host plants. We did not perform congruence tests of the phylogenies of ants and host plants. To date there is no phylogeny available with sufficient resolution of the *Macaranga* sections containing most of the host-plant species colonized by *Decacrema* ants (sections *Pachystemon* s. str. and *Pruinosae* respectively; Blattner et al., 2001; Davies et al., 2001). Matching of phylogenies can therefore only be of limited validity or may even lead towards wrong conclusions (Clark et al., 2000).

Ecological studies showed that most *Decacrema* species colonize not a single but several host plant species that often belong to the same clade

of plants (Fiala et al., 1999; Davies, 2001 for revision of *Macaranga*). Myrmecophytism supposedly evolved several times independently within *Macaranga* (Fiala et al., 1996; Blattner et al., 2001; Davies et al., 2001). However, neither of the three groups within *Decacrema* can be exlusively assigned to a particular clade of *Macaranga* as a whole, as each of the three groups contains mspp. that colonize host-plant species from more than one of the monophyletic groups within *Macaranga* that have evolved myrmecophytism. Thus, host plant spectrum is rather specific for each msp., often independent of their phylogenetic position and most ant species show "clade-specificity" rather than species-specificity. Some msp. colonizing plants from more than one clade (e.g. *C.* cf*. borneensis* or *C. captiosa*) showed no or very little sequence divergence at all which points towards recent host-shifting. At least in these mspp. we can reject cospeciation and strict cocladogenesis between the ants and their host plants as was proposed recently by Itino et al. (2001) for *Macaranga* and their ant associates. However, in studies on specificity and evolution of ant-plant associations the interpretations of results may be strongly influenced by geographic range and choice of species subset (Longino, 1996; Fiala et al., 1999). The interpretation of the *Macaranga*-*Crematogaster* system as a strictly cospeciating system (Itino et al., 2001) is probably due to biased sampling. They sampled ants from nine different plant species comprising rather different groups within *Macaranga* (three of the four different clades within the section *Pachystemon*, one from the section *Pruinosae* and one from the section *Winklerianae*; after Davies, 2001). Thus, if only a single host plant from each clade is considered that is inhabited by an ant taxon specific to this clade, pairings between ants and plants appear to be a monospecific. However, whenever more plants from one clade are sampled species pairings are often less specific, which also happened in their study (Itino et al., 2001).

Similar to other ant-plant systems (overview in Davisdon and McKey, 1993b) plants from the genus *Macaranga* were colonized by different ant taxa several times independently. *Macaranga* has been colonized by ants from two subgenera of *Crematogaster* (*Crematogaster* and *Decacrema*) and several *Camponotus* species (Maschwitz et al., 1996; Federle et al.,

1998a and 1998b). Why the subgenus *Decacrema* radiated strongly, whereas the other taxa have not, is an important question which can help to understand the proximate and ultimate mechanism of speciation in this system.

The data suggest that several aspects play a role in diversification of the subgenus *Decacrema*. I have found evidence for recent host-shifting. Additionally, allopatric speciation can play a major role in diversification of *Decacrema* ants because we found considerable geographic variability within species or species-complexes collected from the same host-plant species from different populations (e.g. *C. decamera*-complex, Figure 7). As species show a constancy in choice of host plant species we would still not exclude sympatric speciation via increased specialization towards a certain host species as one possible mechanism for diversification in some species.

Although, the *Decacrema* species have radiated after the colonization of *Macaranga,* taking all evidence together I would reject a strict cocladogenesis between the *Decacrema* and their *Macaranga* host plants. In future studies I will focus on untangling different mechanisms of speciation and quantifying their respective importance for the diversification within the *Crematogaster*-*Macaranga*-system.

4 Conclusions

The aim of this study was to elucidate the structuring mechanisms leading to the recurring deterministic association patterns found in the *Crematogaster-Macaranga* system.

The phylogenetic analysis, together with the ecological data showed that the *Crematogaster-Macaranga* system has not diversified via strict cocladogenesis. Thus, I assume that association patterns are not a product of strict one-to-one cospeciation.

However, ”diffuse coevolution” between ant species and a group of host plant species seems to be a likely factor influencing the observed association patterns. Most *Decacrema* species colonize more than one host plant species but are not distributed randomly over all myrmecophytic *Macaranga* species. Therefore, ant species may be restricted to a certain spectrum of host plant species and only certain species pairings may be possible. Associations are likely to depend on a match of certain association-related traits of both partners, e.g., morphological characteristics or rates of resource production by the hosts and resource demands by the ant colony. Thus, colonies with high resource demands may not survive on host plants with low resource production. In this respect the third group of organisms that is involved in all *Crematogaster-Macaranga* associations -the coccids- may be important to the associations too. They might play a role in colony development by providing resources (Gaume and McKey, 2002) as they are a trophic link between primary production of the host-plant and the ants.

For *Decacrema* species colonizing several host plant species I would propose that inter- and intraspecific competition of the ants plays a major role in structuring the associations. First, the phylogenetic analysis of the ants suggests that host-shifting has been common in the subgenus *Decacrema*. Secondly, this study shows that competition has a temporal quality that reaches beyond competition for nesting space on saplings. In

all ant-plant systems worldwide –*Macaranga* included- saplings often contain more than one colony founding, which has always been interpreted as a consequence of limited of nesting space (e.g. Davidson et al., 1989; Fonseca, 1993; Fiala et al., 1999). Competition for nesting space on bigger trees seems to be equally high as adult *Macaranga* plants were immediately re-colonized when they had lost ”their” ant-colony. In other ant-plant systems temporal variation due to competition has been documented too (Davidson et al., 1991; Palmer et al., 2000).

Competition during the colony founding phase has been demonstrated to produce association patterns in several ant-plant systems via competition-colonization trade-offs (Janzen, 1975; Yu, 2001). Better colonizers found colonies on saplings as well as on bigger plants but are later displaced by better competitors. Differences in fecundity and dispersal ability of ant queens may also lead to coexistence of several ant species on the same host-plant species.

All the above mentioned mechanisms seem to be relevant in the structuring of the *Crematogaster-Macaranga* association and it is the relative strength of each mechanism that remains to be in question.

The results of this study, together with the extensive former studies on ecology, evolution and biogeography, make the *Crematogaster-Macaranga* ant-plant system the first such species-rich system that is studied in detail from the ant as well as the plant side. This broad basis of knowledge of most aspects of the system make it an ideal model system to go one step further, from only discussing hypothetical models of speciation towards revealing the proximate mechanisms of speciation by field experiments.

5 Summary

One of the most species-rich ant-plant mutualisms worldwide is the palaeotropical *Crematogaster-Macaranga* system. The pioneer-tree genus *Macaranga* (Euphorbiaceae) is mainly inhabited by at least nine specific species of *Crematogaster* (Myrmicinae), of which eight belong to the subgenus *Decacrema*, as well as several species of *Camponotus* (Formicinae). Ant species are not randomly distributed among the *Macaranga* host plants but distinct patterns of associations have been found (Fiala et al., 1999 and references cited therein). The specificity of the associations is maintained in spite of common sympatric distribution of several host-plant species. Associations are, however, usually not species-specific and especially the *Decacrema* ants, that are the focus of this study, usually colonize several host plant species each.

In this study I used a combined approach of ecological data as well as phylogenetic data based on mitochondrial DNA sequences in order to elucidate the factors determining the patterns found in the associations and the evolution of this mutualistic system between the specific *Decacrema* ant partners and their *Macaranga* host plants.

Life history traits of seven different morphospecies found on the most common *Macaranga* host plants were compared and colony development was followed from colony founding on saplings to adult trees. Temporal variability of the associations between *Decacrema* ants and their respective host plants was also examined.

Associations between *Crematogaster* ants of the subgenus *Decacrema* and their *Macaranga* host plants were found to be stable over periods of time, long enough to enable reproduction of the ant colony and (in most cases) the host plants, too. Life-expectancy of the ant colony seems to be shorter than that of the host plant in general. All adult trees still provide nesting space as well as food for the ants.

Colonies from different morphospecies differed in longevity, the onset of alate production, queen number and mode of colony founding. The examined *Decacrema* species could be placed into two groups according

to their life-history traits as well as on morphological grounds: The *decamera*-group and the *captiosa*-group, each named after one species that could be synonymized with one morphospecies included in the group.

Members of the *captiosa*-group have larger colonies, presumably with a longer life-span, and a later onset of reproduction compared to the *decamera*-group. Additionally, queens of the *captiosa*-group found colonies on saplings as well as in the crown region of bigger trees, whereas queens of the *decamera*-group found colonies on saplings and small treelets only. Queens belonging to the *captiosa*-group are brown with relatively large eyes (= 1/3 of the head length), whereas queens from the *decamera*-group are smaller in size, are dark brown to black in colour and have smaller eyes (< 1/3 of the head length).

On some of the host plants examined in this study lifespan of the host plant and their specific ant partners seemed to be well matched whereas on others an ontogenetic succession of specific *Decacrema* partner ants was found, when host plants were abandoned due to the death of comparatively short-lived ant colonies, usually from species belonging to the *decamera*-group. Ant-partners of saplings or young plants often differed from specific partner ants found on bigger trees. Only species belonging to the *captiosa*-group were found to re-colonize the crown region of adult trees, thus facilitating a change of ant species, when long-lived host plant species were colonized by relatively short-lived species from the *decamera*-group first. When long-lived host plants were colonized by long-lived species from the *captiosa*-group associations were stabler: I did not find any temporal variation in ant-inhabitants then.

Life-span of the ant colony as well colony founding behaviour of the different partner ant species therefore play an important role for these ontogenetic changes and the specificity of the associations over time. For the host plant the ontogenetic changes have a strong impact as uninhabited host plants that are not patrolled by workers of specific ant partners suffer higher herbivore damage. Uninhabited host plants may also be colonized by unspecific arboreal ants that only make use of the nesting space and/ or food offered by the plant but do not confer

protection against herbivores. Stable associations with a specific ant partner are therefore most beneficial for the host plants.

Usually ant colonies are monogynous, but changes in the colony structure were found locally in two *Decacrema* species. I found colonies that turned secondarily polygynous, possibly after the death of the original founding queen. Secondary polygyny therefore can prolong the life-span of the ant-colony on its host plant, leading to a parallel life-history and stable association as it was the case in *Macaranga bancana–Crematogaster captiosa*. However, in the other association (*Macaranga hypoleuca–Crematogaster* cf*. decamera*) life-expectancy of the ant-colony is still much shorter than that of its host plant species, leading to a change in the specific ant partner at a later stage.

Pleometrotic foundress associations that directly led to polygynous colonies in one species were also found locally, a phenomenon hardly ever reported from ants in general. Foundress associations were found to be more successful in establishing colonies than single queens. I found indications that this change in colony founding behaviour might be due to interspecific competition for the same host plant species with another *Decacrema* species specific to *Macaranga.*

For the phylogenetic analysis partial mitochondrial cytochrome oxidase I and II were sequenced and Neighbor-Joining, Maximum Parsimony, Maximum Likelihood as well as Bayesian analyses were performed. The four different analyses yielded phenetic as well as phylogenetic trees that all had a similar topology.

Ants of the subgenus *Decacrema* formed a monophyletic clade, indicating a single colonization event at the beginning of the *Macaranga-Decacrema* symbiotic system. In the phylogenetic analysis the *decamera*-group as well as the *captiosa*-group were confirmed and clearly separated from each other. However, two species that would have been placed into the *decamera*-group, due to morphological as well as life-history traits, formed a third separate clade within the *Decacrema*. These two species (msp. 7-

group) as well as the *decamera*-group came out as the basal groups in the phylogenetic analysis. Thus, life-history traits of these two groups (relatively small colonies, early onset of alate production, colony founding in ground region only) would be the ancestral state for *Macaranga*-associated ants of the subgenus *Decacrema*. Changes in colony structure, like secondary polygyny, were found in the *captiosa*- as well as the *decamera*-group and are therefore independent of the affiliation within the phylogeny.

I did not find evidence for strict cocladogenesis between the subgenus *Decacrema* and their *Macaranga* host-plants, although ecological interactions between the two partner groups are close and associations can be rather specific.

The phylogenies presented here, along with the known association patterns indicate that host-shifting of the ants is common in some of the species, opening the possibility of sympatric speciation as a result of increased host usage. Additionally, the considerable geographic substructuring found in the phylogenetic trees suggests that allopatric speciation has played a major role in diversification of the *Decacrema* ants.

6 Zusammenfassung

Das paläotropische *Crematogaster-Macaranga* System bildet eines der weltweit artenreichsten mutualistischen Ameisen-Pflanzen Interaktions-systeme. Es gibt knapp dreißig myrmekophytischen Arten innerhalb der Pionierpflanzengattung *Macaranga* (Euphorbiaceae), welche hauptsächlich von mindestens neun, für diese Pflanzen spezifischen, Ameisen der Gattung *Crematogaster* (Myrmicinae) besiedelt werden. Die Taxonomie der Ameisen ist jedoch nur teilweise geklärt, weshalb ein Großteil der Arten bisher nur in Morphospezies untergliedert wurde. Acht dieser neun Morphospezies gehören der Untergattung *Decacrema* an. Zusätzlich sind einige *Macaranga*-Arten mit Ameisen der Gattung *Camponotus* (Formicinae) assoziiert, die ebenfalls spezifisch für diese Wirtspflanzengattung sind. Die Ameisenarten zeigen keine stochastische Verteilung bei der Besiedlung der *Macaranga*-Wirtspflanzen. Stattdessen finden sich distinkte Verteilungsmuster und spezifische Assoziationen zwischen bestimmten Ameisen- und Pflanzenarten (Fiala et al., 1999 und die darin zitierte Literatur). Diese Verteilungsmuster der Ameisen auf ihren Wirtspflanzen bleiben trotz des häufig sympatrischen Vorkommens mehrerer *Macaranga*-Arten bestehen. Die Assoziationen sind jedoch größtenteils nicht im engeren Sinn artspezifisch, daß eine Ameisenart ausschließlich eine einzige Wirtspflanzenart besiedelt, bzw. jede Pflanzenart ausschließlich mit einer einzigen Ameisenart assoziiert ist. Gerade die Arten der Untergattung *Decacrema*, mit denen sich diese Studie hauptsächlich beschäftigt, besiedeln meist mehrere Wirtspflanzenarten.

Bisher ist sehr wenig darüber bekannt, welche Faktoren für die - vor allem auf Keimlingen und Jungpflanzen nachgewiesenen -Besiedlungsmuster verantwortlich sind und ob und wie lange diese auf größeren Wirtspflanzen erhalten bleiben.

In der vorliegenden Arbeit habe ich deshalb die Strukturierungs-mechanismen der *Crematogaster-Macaranga* Assoziationen auf zwei verschiedenen Ebenen untersucht: sowohl die Stabilität und

Aufrechterhaltung der rezenten Beziehungsmuster als auch mögliche historische Gründe für deren Entstehen. Hierfür habe ich zunächst vergleichend die Dynamik dieser Assoziationen von Jungpflanzen bis hin zu adulten Bäumen untersucht, als auch Aspekte der Evolution des Systems. Für die Untersuchung der Evolution dieses Systems wurde eine Verwandschaftsanalyse der Ameisen der Untergattung *Decacrema* auf molekularer Ebene mit mitochondrialer DNA von Cytochrom-Oxidase I und II durchgeführt. Um mögliche historische Faktoren aufzudecken, die zu diesen Besiedlungsmustern geführt haben könnten, wurden die Ergebnisse der dieser Verwandtschaftsanalyse dann mit dem vorhandenen Stammbaum der Wirtspflanzenarten verglichen und speziell vor dem Hintergrund der ökologischen Daten diskutiert.

Zudem wurden life-history traits (Charakteristika der Lebensgeschichte) von sieben verschiedenen Morphospezies, die auf den häufigsten *Macaranga*-Arten vorkommen vergleichend untersucht, und deren Kolonieentwicklung von der Koloniegründung auf Keimlingen bis hin zu adulten Bäumen erfasst.

Assoziationen zwischen Ameisen der Untergattung Decacrema und ihren Macaranga-Wirtspflanzen waren zumindest so lange stabil, daß sowohl die Ameisen als auch in den meisten Fällen die Wirtspflanzen ihre reproduktive Phase erreichen konnten. Generell scheint die Lebensdauer der Ameisenkolonien kürzer zu sein, als die ihrer Wirtspflanzen. Alle Wirtspflanzen behielten ihre Attraktivität für Ameisen bei, indem sie auch im Adultstadium Nahrung und Nistraum zur Verfügung stellten.

Kolonien der sieben untersuchten Morphospezies unterschieden sich in Lebensdauer, Beginn der Reproduktionsphase, Gynie und der Art der Koloniegründung. Die untersuchten *Decacrema*-Arten können mit Hilfe der Unterschiede in ihren life-history traits, als auch nach ihrer Morphologie in zwei Gruppen unterteilt werden: die *decamera*-Gruppe und die *captiosa*-Gruppe, jeweils benannt nach einer beschriebenen Art innerhalb dieser Gruppe, die mit einer in vorherigen Arbeiten verwendeten Morphospezies synonymisiert werden konnte.

Arten innerhalb der *captiosa*-Gruppe haben, im Vergleich zu Arten der *decamera*-Gruppe, größere Kolonien, wahrscheinlich eine längere Lebensdauer und erreichen ihre reproduktive Phase später. Königinnen der *captiosa*-Gruppe können sowohl in Keimlingen als auch in der Kronenregion größerer Bäume Kolonien gründen, wohingegen gründende Königinnen der *decamera*-Gruppe ausschließlich bodennah auf Keimlingen und kleineren Bäumen gefunden wurden. Zudem unterscheiden sich die Königinnen von Arten der beiden Gruppen in ihrer Morphologie: Königinnen der *captiosa*-Gruppe sind bräunlich gefärbt und haben relativ große Komplexaugen (= 1/3 der Kopflänge), während Königinnen der *decamera*-Gruppe relativ klein und dunkelbraun bis schwarz gefärbt sind. Zudem haben sie relativ kleinere Komplexaugen (< 1/3 der Kopflänge).

Bei einigen der untersuchten Assoziationen scheinen die Lebensdauer der Wirtspflanzen und ihrer spezifischen Ameisenkolonien gut aufeinander abgestimmt zu sein, wohingegen bei anderen eine ontogenetische Sukzession von verschiedenen spezifischen *Decacrema*-Arten gefunden wurde. Dies war vor allem dann der Fall, wenn Wirtspflanzen zunächst von Arten der *decamera*-Gruppe besiedelt waren, deren relativ kurzlebige Kolonien früh abstarben. Da nur Königinnen von Arten der *captiosa*-Gruppe auch in der Kronenregion größerer Bäume Kolonien gründen können, kommt es in diesen Fällen zu einem Wechsel in der Ameisenbesiedlung. Die Assoziationen zwischen langlebigen Wirtspflanzenarten und den langlebigeren Kolonien von Arten der *captiosa*-Gruppe waren stabiler. Bei diesen Assoziationen wurde kein Wechsel der spezifischen Ameisenart über die Zeit festgestellt.

Die Lebensdauer der Ameisenkolonien sowie das Gründungsverhalten von Königinnen spielen deshalb eine wichtige Rolle bei der ontogenetischen Sukzession der Ameisenbesiedler auf den Wirtspflanzen. Die ontogenetischen Wechsel in der Besiedlung sind für die Wirtspflanzen von großer Bedeutung, denn in Zeiten, in denen sie nicht von einer intakten und der Größe der Pflanze entsprechenden Kolonie bewohnt sind, fehlt ihnen der Schutzeffekt der Ameisen gegen Herbivorie.

Unbewohnte Bäume können sowohl von spezifischen *Decacrema*-Arten der *captiosa*-Gruppe wiederbesiedelt werden als auch von unspezifischen arborealen Ameisenarten, die zwar den angebotenen Nistraum und/ oder Nahrung nutzen, jedoch keinen Herbivorieschutz gewähren. Aus diesem Grund sind möglichst stabile Assoziationen mit einer spezifischen *Decacrema*-Art für die Wirtspflanze von Vorteil.

Kolonien der *Decacrema*-Arten sind normalerweise monogyn. Lokal wurden jedoch Kolonien von zwei Arten entdeckt, die –wahrscheinlich nach dem Tod der ursprünglichen Königin sekundär polygyn waren, d.h. mehrere reproduktive Königinnen besaßen. Da durch sekundäre Polygynie die Lebens- und Verweildauer einer Kolonie auf einer Wirtspflanze verlängert wird, bleiben Assoziationen länger stabil, im Extremfall bis hin zu einer ähnlichen Lebensdauer von Wirtspflanze und Partnerkolonie. Ein solcher ”paralleler Lebens zyklus” von Wirtspflanze und spezifischer Partnerameise wird so in der Assoziation zwischen *Macaranga bancana–Crematogaster captiosa* erreicht. Allerdings war bei einer zweiten Art, bei der sekundäre Polygynie gefunden wurde (*Crematogaster* cf. *decamera* auf *Macaranga hypoleuca*), die Lebensdauer der Kolonie geringer als die der Wirtspflanze. In dieser Assoziation kam es deshalb wiederum zu einem Wechsel in der Ameisenbesiedlung bei größeren Bäumen.

Pleometrotisches Gründungsverhalten, d.h. daß mehrere Königinnen gemeinsam eine Kolonie gründen, wurde lokal bei einer Art gefunden. Bei diesen Gründungsassoziationen kam es nicht zu einer Dezimierung der Königinnen durch Kampf nach dem Schlüpfen der ersten Arbeiterinnen, sondern die Kolonien blieben polygyn. Dies ist ein sehr seltenes Verhalten, welches bisher gerenell bei Ameisen kaum beobachtet wurde. Im Vergleich zu haplometrotisch, d.h. alleine gründenden Königinnen waren diese Assoziationen erfolgreicher bei der Etablierung von Kolonien auf Jungpflanzen. Der Wechsel im Verhalten bei der Koloniegründung hin zu Pleometrosen ist wahrscheinlich auf starke interspezifsiche Konkurrenz um Nistraum zurückzuführen.

Teile der Sequenzen der mitochondrialen Gene Cytochrom Oxidase I und II (483 bzw. 439 Basenpaare) wurden für eine phylogenetische Analyse der besiedelnden Ameisen der Untergattung *Decacrema* verwendet. Die mit vier verschiedenen Methoden zur Verwandtschaftsanalyse erstellten Stammbäume (Neighbor-Joining, Maximum Parsimony, Maximum Likelihood und einer Bayesischen Analyse) unterschieden sich nicht in ihrer Topologie.

In allen Stammbäumen bildeten die Ameisenarten der Untergattung *Decacrema* eine monophyletische Gruppe. Dies deutet darauf hin, daß die Kolonisierung von *Macaranga*-Wirtspflanzen durch Ameisen dieser Untergattung ein einmaliges Ereignis war, gefolgt von einer Radiation der *Decacrema*-Arten. In der phylogenetischen Analyse bestätigte sich die Monophylie der *decamera*- und die *captiosa*-Gruppe. Allerdings waren in allen Analysen zwei Arten klar abgetrennt und bildeten eine dritte Gruppe (Msp. 7-Gruppe). Diese beiden Arten zeigten die charakteristischen morphologischen und life-history Merkmale von Arten der *decamera*-Gruppe. In der Verwandtschaftsanalyse erscheinen die Msp. 7- und die *decamera*-Gruppe als die basalen Gruppen innerhalb der *Decacrema*-Arten. Die ursprünglichen Merkmale der *Macaranga*-assoziierten Ameisen der Untergattung *Decacrema* wären dementsprechend relativ kleine, kurzlebige Kolonien, die früh die reproduktive Phase erreichen, sowie ein ausschließlich bodennahes Gründen von Kolonien. Wechsel in der Koloniestruktur, wie etwa sekundäre Polygynie, wurde sowohl innerhalb der *captiosa*- als auch der *decamera*-Gruppe gefunden und scheinen deshalb unabhängig von der Stellung innerhalb der Phylogenie zu sein.

Ich fand keine Hinweise für eine strikte Kocladogenese zwischen den Ameisen der Untergattung *Decacrema* und deren *Macaranga*-Wirtspflanzen, trotz der hohen Spezifität der Assoziationen der beiden Partner und ihrer mannigfaltigen und engen Wechselbeziehungen. Speziell vor dem Hintergrund der bekannten Besiedlungsmuster der *Crematogaster-Macaranga*-Assoziationen zeigt ein Vergleich der Stammbäume der *Decacrema*-Arten und der *Macaranga*-Wirtspflanzen deutlich, daß offensichtlich Wirtswechsel bei der Evolution des Systems eine große Rolle gespielt haben. Die Auftrennung einer Ameisenart auf

zwei verschiedene Pflanzenarten durch Wirtswechsel eröffnet die Möglichkeit der sympatrischen Artbildung als Folge von verstärkter Wirtsnutzung und Anpassung an den jeweiligen Wirt. Die in der Verwandtschaftsanalyse gefundene geographische Substrukturierung der Ameisenpopulationen weist darauf hin, daß auch allopatrische Artbildung bei der Speziation der *Decacrema*-Arten eine wichtige Rolle gespielt hat bzw. noch spielt.

7 References

André, E. (1896). Fourmis nouvelles d´Asie et d´Australie. *Rev. Ent. Caen* 15: 251-265.

Ayala, F.J., Wetterer, J.K., Longino, J.T. and Hartl, D.L. (1996). Molecular phylogeny of *Azteca* ants (Hymenoptera: Formicidae) and the colonization of *Cecropia* trees. *Mol. Phyl. Evol*. 5 (2): 423-428.

Agosti, D., Moog, J. and Maschwitz, U. (1999). Revision of the oriental plant-ant genus *Cladomyrma*. *Novitates* 3283, 24 pp.

Baker, J.A. (1934). Notes on the biology of *Macaranga* spp.. *Gardens Bulletin Straits Settlement* 8: 63-68.

Beattie, A.J. (1985). *The Evolutionary Ecology of Ant-plant Mutualism*. Cambridge Univ. Press, Cambridge, UK.

Benson, W.W. (1985). Amazon ant-plants. In: *Amazonia* (G.T. Prance and T.E. Lovejoy, Eds.), Pergamon Press New York, pp. 239-266.

Bernasconi, G. and Strassmann, J.E. (1999). Cooperation among unrelated individuals: the ant foundress case. *TREE* 14: 477-482.

Blattner, F.R., Weising, K., Bänfer, G., Maschwitz, U. and Fiala, B. (2001). Molecular analysis of phylogenetic relationships among myrmecophytic *Macaranga* species (Euphorbiaceae). *Mol. Phyl. Evol*. 19: 331-344.

Bolton, B. (1995). *A new general catalogue of the ants of the world*. Harvard University Press, Cambridge, Massachusetts, London, England.

Brady S.G., Gadau, J. and Ward P.S. (2000). Systematics of the ant genus *Camponotus* (Hymenoptera: Formicidae): A preliminary analysis using data from the mitochondrial gene cytochrome oxidase I. In: *Hymenoptera: Evolution, Biodiversity and Biological Control.* (A. Austin and M. Dowton, Eds.), CSIRO Publishing, Canberra, pp.131-139.

Brooks, D.R. and McLennan, D.A. (1991). *Phylogeny, ecology and behaviour.* University of Chicago Press, Chicago.

Brouat, C., Garcia, N., Andary, C. and McKey, D. (2001a). Plant lock and ant key: pairwise coevolution of an exclusion filter in an ant-plant mutualism. *Proc. R. Soc. Lond. B* 268: 2131-2141.

Brouat, C., Gielly, L. and McKey, D. (2001b). Phylogenetic relationships in the genus *Leonardoxa* (Leguminosae: Cesalpinioideae) inferred from chloroplast *trnL* Intron and *trnL-trn-F* intergenic spacer sequences. *Am. J. Bot.* 88: 143-149.

Buckley, R.C. (1982). Ant-plant interactions: a world review. In: *Ant-plant interactions in Australia* (R.C. Buckley, Ed.), Dr. W. Junk Publishers, The Hague, pp. 111-141.

Chapman J.W. and Capco, S.R. (1951). *Checklist of the ants (Hymenoptera, Formicidae) of Asia*. Manila, Bureau of Printing.

Chenuil, A. and McKey, D.B. (1996). Molecular phylogenetic study of a myrmecophyte symbiosis: Did *Leonardoxa* / ant associations diversify via cospeciation? *Mol. Phyl. Evol*. 6: 270-286.

Choe, J.C. and Perlman, D.L. (1997). Social conflict and cooperation among founding queens in ants. In: *The evolution of social behaviour in insects and arachnids* (J.C. Choe and B.J. Crespi, Eds.), Cambridge, Cambridge University Press, pp. 316-332.

Clark, M.A., Moran, N., Baumann, P. and Wernegreen, J. (2000). Cospeciation between bacterial endosymbionts (*Buchnera*) and a recent radiation of aphids (*Uroleucon*) and pitfalls of testing for phylogenetic congruence. *Evolution* 54: 517-525.

Crozier, R.H. and Crozier, Y.C. (1993). The mitochondrial genome of the honeybee *Apis mellifera*: Complete sequence and genome organization. *Genetics* 133: 97-117.

Crozier, R.H. and Page, R.E. (1985). On being the right size: male contributions and multiple mating in social Hymenoptera. *Behav. Ecol. Sociobiol*. 18: 105-115.

Cunningham, C.W. (1997). Can three incongruence tests predict when data should be combined? *Mol. Biol. Evol*. 14: 733-740.

Davidson, D.W. and Fisher, B.L. (1991). Symbioses of ants with *Cecropia* as a function of light regime. In: *Ant-plant interactions* (C.R. Huxley and D.K. Cutler, Eds.), Oxford University Press, Oxford, pp. 289-309.

Davidson, D.W., Foster, R.B., Snelling, R.R. and Lozada, P.W. (1991). Variable composition of some tropical ant-plant symbioses. In: *Plant-animal interactions: Evolutionary ecology in tropical and temperate regions* (P.W. Price, T.M. Lewinsohn, G.W. Fernandes and W.W. Benson, Eds.), John Wiley & Sons, Inc., New York, pp. 145-162.

Davidson, D.W. and McKey, D. (1993a). Ant-plant symbioses: Stalking the Chuyachaqui. *TREE* 8: 326-332.

Davidson, D.W. and McKey, D. (1993b). The evolutionary ecology of symbiotic ant-plant relationships. *J. Hym. Res*. 2: 13-83.

Davidson, D.W., Snelling, R.R. and Longino, R.T. (1989). Competition among ants for myrmecophytes and the significance of plant trichomes. *Biotropica* 21: 64-73.

Davies, S.J. (1999). New species of *Macaranga* (Euphorbiaceae) section *Pachystemon* from Borneo. *Kew Bulletin* 54: 147-154.

Davies, S.J. (2001). Systematics of *Macaranga* sects. *Pachystemon* and *Pruinosae* (Euphorbiaceae). *Harv. Pap. Bot.* 6: 371-448.

Davies, S.J., Lum, S.K.Y., Chan, R. and Wang, L.K. (2001). Evolution of myrmecophytism in Western Malesian *Macaranga* (Euphorbiaceae). *Evolution* 55: 1542-1559.

Davies, S.J., Palmiotto, P.A., Ashton, P.S., Lee, H.S. and LaFrankie, J.V. (1998). Comparative ecology of 11 sympatric species of *Macaranga* in Borneo: tree distribution in relation to horizontal and vertical resource heterogeneity. *J. Ecol*. 86: 662-673.

Emery, C. (1921) Hymenoptera. Fam. Formicidae. Subfam. Myrmicinae. *Genera Insectorum* 174: 1-397.

Federle, W. (1998). Strukturmechanismen der Lebensgemeinschaft auf einer Ameisenpflanze. PhD-thesis, Julius-Maximilians-University Wuerzburg.

Federle, W., Fiala, B. and Maschwitz, U. (1998a). Camponotus (Colobopsis) and Macaranga: A specific two partner ant-plant system from Malaysia. *Tropical Zoology* 11: 83-94.

Federle, W., Maschwitz, U. and Fiala, B. (1998b). The two-partner ant-plant system of *Camponotus* (*Colobopsis*) sp. 1 and *Macaranga puncticulata* (Formicidae: Formicinae; Euphorbiaceae): Myrmecophytic traits of the partner ant. *Insect. Soc*. 45: 1-16.

Federle, W., Maschwitz, U., Fiala, B., Riederer, M. and Hölldobler, B. (1997). Slippery ant-plants and skilful climbers: Selection and protection of specific ant partners by epicuticular wax blooms in *Macaranga* (Euphorbiaceae). *Oecologia* 112: 217-224.

Feldhaar, H., Fiala, B., Gadau, J. and Maschwitz, U. (2002). How life-history traits of the ant partner influence the specificity of the *Crematogaster-Macaranga* association. Proc. XV. Annual Meeting of Gesellschaft für Tropenökologie (GTÖ), Göttingen, Germany, p. 42.

Feldhaar, H., Fiala, B., Rosli bin Hashim and Maschwitz, U. (2000). Maintaining an ant-plant symbiosis: secondary polygyny in the *Macaranga triloba-Crematogaster* sp. association. *Naturwissenschaften* 87: 408-411.

Felsenstein, J. (1981). Evolutionary trees from DNA sequences: A maximum likelihood approach. *J. Mol. Evol*. 17: 368-376.

Fiala, B. (1988). Biologie, Funktion und Evolution eines malaysischen Myrmekophytiesystems. Unpublished D. Phil. Thesis, University of Frankfurt.

Fiala, B. (1996). Ants benefit pioneer trees: The genus *Macaranga* as an example of ant-plant associations in dipterocarp forest ecosystems. In: *Dipterocarp forest ecosystems: Towards sustainable management*. (E. Schulte and D. Schöne, Eds.), World Scientific, Singapore, pp. 102-123.

Fiala, B., Grunsky, H., Maschwitz, U. and Linsenmair, K.E. (1994). Diversity of ant-plant interactions: Protective efficacy in *Macaranga* species with different degrees of ant-associations. *Oecologia* 97: 186-192.

Fiala, B., Jakob, A., Maschwitz, U. and Linsenmair, K.E. (1999). Diversity, evolutionary specialization and geographic distribution of a mutualistic ant-plant complex: *Macaranga* and *Crematogaster* in South East Asia. *Biol. J. Linn. Soc*. 66: 305-331.

Fiala, B. and Maschwitz, U. (1990). Studies on the South East Asian ant-plant association *Crematogaster borneensis* / *Macaranga*: Adaptations of the ant partner. *Insect. Soc*.: 212-231.

Fiala, B. and Maschwitz, U. (1991). Extrafloral nectaries in the genus *Macaranga* (Euphorbiaceae) in Malaysia: comparative studies of their possible significance as predispositions for myrmecophytism. *Biol. J. Linn. Soc.* 44: 287-305.

Fiala, B. and Maschwitz, U. (1992). Food bodies and their significance for the obligate ant-association in the tree genus *Macaranga* (Euphorbiaceae). *Bot. J. Linn. Soc*. 110: 61-75.

Fiala, B., Maschwitz, U. and Linsenmair, K.E. (1996). *Macaranga caladiifolia*, a new type of ant-plant among Southeast Asian myrmecophytic *Macaranga* species. *Biotropica* 28: 408-412.

Fiala, B., Maschwitz, U., Tho, Y.P. and A.J. Helbig (1989). Studies of a South East Asian ant-plant association: protection of *Macaranga* trees by *Crematogaster borneensis*. *Oecologia* 79: 463-470.

Fonseca, C.R. (1993). Nesting space limits colony size of the plant-ant *Pseudomyrmex concolor*. *Oikos* 67: 473-482.

Fonseca, C.R. (1999). Amazonian ant-plant interactions and the nesting space limitation hypothesis. *J.Trop. Ecol*. 15: 807-825.

Fonseca, C.R. and Benson, W.W. (1995). Ontogenetic succession on Amazonian ant-trees. *Bull. Ecol. Soc. Amer*. 76 (2 suppl. part 2): 83.

Fonseca, C.R. and Ganade, G. (1996). Asymmetries, compartments and null interactions in an Amazonian ant-plant community. *J. Animal Ecol*. 65: 339-347.

Forel, A. (1910). Glanures myrmécologiques. *Ann. Soc. Entomol. Belg*. 54: 6-32.

Forel, A. (1911). Fourmis de Borneo, Singapore, Ceylan etc. récoltées par MM. Haviland, Green, Winkler, Will, Hose, Roepke et Waldo. *Rev. Suisse Zool*. 19 (2): 23-62.

Gaume, L. and McKey, D. (1999). An ant-plant mutualism and its host-specific parasite: activity rhythms, young leaf patroling, and effects on herbivores of two specialist plant-ants inhabiting the same myrmecophyte. *Oikos* 84: 130-144.

Gaume, L. and McKey, D. (2002). How identity of the homopteran trophobiont affects sex allocation in a symbiotic plant-ant: the proximate role of food. *Behav. Ecol. Sociobiol*. 51: 197-205.

Gaume, L., McKey, D. and Anstett, M.-C. (1997). Benefits conferred by ”timid” ants: active anti-herbivore protection of the rainforest tree *Leonardoxa africana* by the minute ant *Petalomyrmex phylax*. *Oecologia* 112: 209-216.

Hasegawa, M., Kishino, H. and Yano, T. (1985). Dating of the human-ape splitting by a molecular clock of mitochondrial DNA. *J. Mol. Evol*. 21: 160-174.

Heckroth, H.P. (2000). *Schildläuse in einer myrmekophytischen Drei-Partner-Symbiose: Untersuchungen zur Sozioökologie von Cocciden (Hemiptera: Coccoidae) in der südostasiatischen Macaranga (Euphorbiaceae) – Crematogaster (Hymenoptera: Formicidae) Ameisen-Pflanzen-Assoziation*. GCA-Verlag, Herdecke.

Heckroth, H.P., Fiala, B., Gullan, P., Maschwitz, U. and Azarae, I.Hj. (1998). The soft scale (Coccidae) associates of Malaysian ant-plants. *J. Trop. Ecol.* 14: 1-18.

Heil, M., Fiala, B., Linsenmair, K.E., Zotz, G., Menke, P. and Maschwitz, U. (1997). Food body production in *Macaranga triloba* (Euphorbiaceae): a

plant investment in anti-herbivore defence via symbiotic ant partners. *J. Ecol.* 85: 847-861.

Heil, M., Fiala, B., Maschwitz, U. and Linsenmair, K.E. (2001a). On the benefits of indirect defence: Short- and long-term studies in antiherbivore protection via mutualistic ants. *Oecologia* 126: 395-403.

Heil, M., Hilpert, A., Fiala, B. and Linsenmair, K.E. (2001b). Nutrient availability and indirect (biotic) defence in a Malaysian ant-plant. *Oecologia* 126: 404-408.

Herbers, J.M. (1993). Ecological determinants of queen number in ants. In: *Queen number and sociality in insects* (L. Keller, Ed.), Oxford University Press, Oxford, pp. 262-293.

Hillis, D.M. and Huelsenbeck, J.P. (1992). Signal noise, and reliability in molecular phylogenetic analyses. *J. Hered*. 83: 189-195.

Hillis, D.M. and Bull, J.J. (1993). An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analysis. *Syst. Biol*. 42: 182-192.

Hölldobler, B. and Wilson, E.O. (1990). *The Ants*. Belknap Press, Cambridge, Massachusetts.

Huelsenbeck, J.P. (2000). ”Mr Bayes: Bayesian inference of phylogeny” distributed by the author, Department of Biology, University of Rochester, NY.

Huelsenbeck, J.P., Ronquist, F., Nielsen, R. and Bollback, J.P. (2001). Bayesian inference of phylogeny and its impact on evolutionary biology. *Science* 294: 2310-2314.

Inui, Y., Itioka, T., Murase, K., Yamaoka, R. and Itino, T. (2001). Chemical recognition of partner plant species by foundress ant queens in *Macaranga-Crematogaster* myrmecophytism. *Journ. Chem. Ecol*. 27: 2029-2040.

Itino, T., Davies, S.J., Tada, H., Inoguchi, M., Itioka, T., Yamane, S. and Inoue, T. (2001). Cospeciation of ants and plants. *Ecol. Res.* 16: 787-793.

Itioka, T., Nomura, M., Inui, Y., Itino, T. and Inoue, T. (2000). Difference in intensity of ant defense among three species of *Macaranga* myrmecophytes in a Southeast Asian dipterocarp forest. *Biotropica* 32: 318-326.

Janzen, H.D. (1973). Evolution of polygynous obligate acacia-ants in western Mexico. *J. Animal Ecol*. 42: 727-750.

Janzen, H.D. (1975). *Pseudomyrmex nigripilosa*: a parasite of a mutualism. *Science* 188: 936-937.

Jordano, P. (1987). Patterns of mutualistic interactions in pollination and seed dispersal: Connectance, dependence asymmetries, and coevolution. *Am. Nat*. 129: 657-677.

Kaufmann, E., Weissflog, A., Hashim, R. and Maschwitz, U. (2001). Ant-gardens on the giant bamboo *Gigantochloa scortechinii* (Poaceae) in West-Malaysia. *Insect. Soc*. 48: 125-133.

Longino, J.T. (1989). Geographic variation and community structure in an ant-plant mutualism: *Azteca* and *Cecropia* in Costa Rica. *Biotropica* 21: 126-132.

Longino, J.T. (1991). *Azteca* ants in *Cecropia* trees: taxonomy, colony structure and behaviour. In: *Ant-plant interactions* (C.R. Huxley and D.K. Cutler, Eds.), Oxford University Press, Oxford, pp. 271-288.

Longino, J.T. (1996). Taxonomic characterization of some live-stem inhabiting *Azteca* (Hymenoptera: Formicidae) in Costa Rica, with special reference to the ants of *Cordia* (Boraginaceae) and *Triplaris* (Polygonaceae). *J. Hym. Res.* 5: 131-156.

Maschwitz, U., Fiala, B., Davies, S.J. and Linsenmair, K.E. (1996). *Camponotus* and *Crematogaster* as partners of one myrmecophyte: A new three-partner association in the genus *Macaranga* from Borneo (including description of *Camponotus macarangae*, new species by K. Dumpert). *Ecotropica* 2: 20-40.

Maynard Smith, J. (1998). Evolutionary genetics. Oxford University Press, Oxford.

McKey, D. (1984). Interaction of the ant-plant *Leonardoxa africana* (Caesalpiniaceae) with its obligate inhabitants in a rainforest in Cameroon. *Biotropica* 16: 81-99.

McKey, D, Gaume, L. and Dalecky, A. (1999). Les symbioses entre plantes et fourmis arboricoles. *Année Biol*. 38: 169-194.

Mintzer, A.C. (1987). Primary polygyny in the ant *Atta texana*: number and weight of females and colony foundation success in the laboratory*. Insect. Soc*. 34: 108-117.

Moog, J., Drude, T. and Maschwitz, U. (1998). Protective function of the plant-ant *Cladomyrma maschwitzi* to its host, *Crypteronia griffithii*, and the dissolution of the mutualism (Hymenoptera: Formicidae). *Sociobiology* 31: 105-129.

Moog, U., Fiala, B., Federle, W. and Maschwitz, U. (2002). Thrips pollination of the dioeceous ant-plant *Macaranga hullettii* (Euphorbiaceae) in Southeast Asia. *Am. J. Bot.* 89: 50-59.

Morley, R.J. (2000). *Origin and Evolution of Tropical Rain Forests*. Chichester, John Wiley and Sons Ltd.

Palmer, T.M., Young, T.P., Stanton, M.L. and Wenk, E. (2000). Short-term dynamics of an acacia ant community in Laikipia, Kenya. *Oecologia* 123: 425-435.

Perlman, D.L. (1992). Colony founding among *Azteca* ants. PhD Thesis, Harvard University, Cambridge, Mass.

Posada, D. and Crandall, K.A. (1998). Modeltest: Testing the model of of DNA substitution. *Bioinformatics* 14: 817-818.

Primack, R.B. and Lee, H.S. (1991). Population dynamics of pioneer (*Macaranga*) trees and understory (*Mallotus*) trees in primary and selectively logged Bornean rain forests. *J. Trop. Ecol*. 7: 439-458.

Sambrook, J., Fritsch, E.F. and Maniatis, T. (eds.) (1989). *Molecular cloning: A laboratory manual*. 2nd edn. Laboratory Press, Cold Spring Harbor.

Schluter, D. (2000). *The biology of adaptive radiations*. Oxford University Press, Oxford.

Schluter, D. (2001). Ecology and the origin of species. TREE 16: 372-380.

Simon, C., Frati, F., Beckenbach, A., Crespi, B., Lui, H. and Flook, P. (1994). Evolution, weighting, and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. *Entomol. Soc. Am*. 87: 651-701.

Slik, F.J.W. and van Welzen, P.C. (2001) A phylogeny of *Mallotus* (Euphorbiaceae) based on morphology: Indications for a pioneer origin of *Macaranga*. *Syst. Bot.* 26: 786-796.

Sommer, K. and Hölldobler, B. (1995). Colony founding by queen association and determinants of reduction in queen number in the ant *Lasius niger. Anim. Behav*. 50: 287-294.

Strassmann, J. (2001). The rarity of multiple mating by females in the social Hymenoptera. *Insect. Soc*. 48: 1-13.

Swofford, D.L. (2002). ”PAUP*, Phylogenetic Analysis Using Parsimony (*and other methods), Version 4.0b10”. Sinauer Associates, Sunderland, Massachusetts.

Swofford, D.L., Olsen, G.J., Waddell, P.J. and Hillis, D.M. (1996). Phylogenetic Inference. In: *Molecular Systematics*. (D.M., Hillis, C. Moritz and B.K. Mable, Eds.), 2nd ed., Sinauer Associates, Sunderland, Massachusetts, pp. 407-515.

Tho, Y.P. (1978). Living in harmony. *Nature Malaysiana* 3: 34-39.

Vasconcelos, H.L. (1990). The relationship between plant size and ant association in the ant plant *Maieta guianensis*. Annual Meeting of the British Ecological Society, Manchester, England.

Trunzer, B., Heinze, J. and Hölldobler, B. (1998). Cooperative colony founding and experimental primary polygyny in the ponerine ant *Pachycondyla villosa*. *Insect. Soc*. 45: 267-276.

Vasconcelos, H. (1993). Ant colonization of *Maieta guianensis* seedlings, an Amazon ant-plant. *Oecologia* 95: 439-443.

Verhaagh, M. (1994). *Pachycondyla luteola* (Hymenoptera, Formicidae), an inhabitant of *Cecropia* trees in Peru. *andrias* 13: 215-224.

Viehmeyer, H. (1916). Ameisen von Singapore. *Arch. f. Naturg*. 81, p. 126.

Ward, P.S. (1991). Phylogenetic analysis of pseudomyrmecine ants associated with domatia-bearing plants. In: *Ant-plant interactions*. (C.R. Huxley and D.F. Cutler, Eds.), Oxford, Oxford University Press, pp. 335-352.

Ward, P.S. (1993). Systematic studies on *Pseudomyrmex* acacia-ants. *J. Hym. Res*. 2: 117-168.

Ward, P.S. (1999). Systematics, biogeography and host plant associations of the *Pseudomyrmex viduus* group (Hymenoptera: Formicidae), *Triplaris*- and *Tachigali*-inhabiting ants. *Zool. J. Linn. Soc*. 126: 451-540.

Whitmore, T.C. (1969). First thoughts on species evolution in Malayan *Macaranga* (Studies on *Macaranga* III). *Biol. J. Linn. Soc*. 1: 223-231.

Whitmore, T.C. (1975). *Macaranga*. In: *The Euphorbiaceae of Borneo* (H.K. Airy-Shaw, Ed.), pp. 140-159.

Whitmore, T.C. (1981). *Macaranga* in New Guinea and the Bismarck Archipelago. *Kew Bull.* 34: 599-606.

Whitmore, T.C. (1984). *Tropical rain forests in the Far East*. 2nd Edition, Claredon Press, Oxford.

Wetterer, J.K., Schultz, T.R. and Meier, R. (1998). Phylogeny of fungus-growing ants (Tribe Attini) based on mtDNA sequence and morphology. *Mol. Phylogenet. Evol*. 9: 42-47.

Whittingham, L.A., Slikas, B., Winkler, D.W. and Sheldon, F.H. (2002). Phylogeny of the tree swallow genus, *Tachycineta* (Aves: Hirundinidae), by the Bayesian analysis of mitochondrial DNA sequences. *Mol. Phylogenet. Evol*. 22: 430-441.

Young, T.P., Stubblefield, C.H. and Isbell, L.A. (1997). Ants on swollen-thorn acacias: species coexistence in a simple system. *Oecologia* 115: 508-513.

Yu, D.W. (2001). Parasites of mutualism. *Biol. J. Linn. Soc.* 72: 529-546.

Yu, D.W. and Davidson, D.W. (1997). Experimental studies of species-specificity in *Cecropia*-ant relationships. *Ecol. Monogr*. 67: 273-294.

Yu, D.W. and Wilson, H.B. (2001). The competition-colonization trade-off is dead; long live the competition-colonization trade off. *Am. Nat*. 158 (1): 49-63.

8 Acknowledgements

First of all, I would like to thank Prof. Dr. U. Maschwitz and Dr. B. Fiala for their support of every stage of my work. I deeply appreciate their opinion-sharing in numerous important discussions, their encouragement to carry out my ideas, and their assistance in the realization of my research both by advice and financial support.

I am very grateful to Dr. J. Gadau for the opportunity to do the molecular phylogeny in his laboratory. He and his group, especially Christoph Strehl and Karin Möller, were very helpful and patient introducing me to the lab.

My special thanks goes to members of the group in Frankfurt, especially Volker Witte and Eva Kaufmann, for making field trips to Malaysia fun and for the improvement of my knowledge of the Malayan snake fauna.

People in Würzburg as well as the atmosphere in Prof. Hölldoblers group contributed very much to the fact that I became a whole-hearted biologist: Special thanks to Brigitte, Jürgen, Christoph and Dunja.

This work would not have been possible without the infrastructure provided by counterparts in Malaysia. I am therefore thankful to Assoc. Prof. Rosli bin Hashim from University Malaya, Kuala Lumpur and Prof. Dr. Maryati Mohamed from University Malaysia Sabah in Kota Kinabalu as well as Sabah Parks, namely Assistant Director Dr. Jamili Nais. I am grateful to the Economic Planning Unit (EPU) at the Prime Minister´s Department for granting a research permit.

I would like to thank Bah Tera and Ahmad for afternoon talks on the veranda. I am thankful to Assoc. Prof. F. Ito for showing me how to dissect spermathecae.

Finally I would like to thank my closest friends, especially Tanja Brühl, for giving me support during the whole time of this thesis whenever it was needed.

This work was accomplished in memory of my colleague Thomas Drude, who had a fatal accident when starting his thesis on this very topic. I would have loved to discuss the work with him and share ideas.

Financial support for this work came from the DAAD as well as DFG (projects MA 373/ 20-1, FI 606/ 4-1 and GA 661/2-1).

9 Appendix

Nexus block and assumption block for GTR-model with site-specific rates

Nexus and assumption block for 27 taxa, comprising 922 bp, starting with first codon position. Codon position are set with the charset-command. The GTR –model is set by nst=6, allowing six different substitions in the DNA.

```
#NEXUS

Begin data;
        Dimensions ntax=27 nchar=922;
        Format datatype=dna gap=- missing=?;
        Matrix

Datamatrix in NEXUS format
        ;
End;

begin mrbayes;
set autoclose=yes;
        charset first_pos  = 1-922\3;
        charset second_pos = 2-922\3;
        charset third_pos  = 3-922\3;
        partition by_codon = 3:first_pos,second_pos,third_pos;
        lset nst=6 rates=sitespec sitepartition=by_codon;
        mcmcp ngen=1000000 printfreq=100 samplefreq=100 nchains=4
savebrlens=yes;
end;
```

Nexus and assumption block for GTR-"invariant+gamma" -model

In this submodelmodel of the GTR model, a number of sites remains invariable over all taxa whereas the variable sites follow a gamma-distribution (term: rates=invgamma).

```
#NEXUS

Begin data;
        Dimensions ntax=27 nchar=922;
        Format datatype=dna gap=- missing=?;
        Matrix

Datamatrix in NEXUS format
        ;
End;

begin mrbayes;
set autoclose=yes;
        charset first_pos  = 1-922\3;
        charset second_pos = 2-922\3;
        charset third_pos  = 3-922\3;
        partition by_codon = 3:first_pos,second_pos,third_pos;
        lset nst=6 rates=invgamma basefreq=estimate
sitepartition=by_codon;

        mcmcp ngen=500000 printfreq=100 samplefreq=100 nchains=4
savebrlens=yes;
end;
```

10 Curriculum vitae

Name:	Heike B. Feldhaar
Date of birth:	19th of May 1970
Place of birth:	Frankfurt/ Main, Germany
Nationality:	German

10.1 Education

May 1989:	Abitur at the Gymnasium Alkönigschule Kronberg
October 1989 - October 1996:	Studies at the Johann Wolfgang Goethe-University Frankfurt in biology
October 1991:	Vordiploma in zoology, botany, chemistry and physics
(Interruption of University studies:	Bicycle trip across Canada 2/92 to 10/92)
October 1996:	Submission of diploma-thesis with the title ”Untersuchungen zur Ameisenbesiedlung der paläo-tropischen Rutacee *Zanthoxylum myriacanthum*”, Advisor: Prof. U. Maschwitz

November 1996 – December 1997:	Research assistance at the Medical Department of the J.W. Goethe-University (Gastro-enterology), working with electro-physiology and heat-shock proteins of gastrointestinal cell-lines
January 1998:	Start of the PhD-thesis in Frankfurt at the J.W. Goethe-University under supervision of Prof. U. Maschwitz/ Dr. B. Fiala of the J.-M. University of Würzburg

10.2 Miscellanous

Languages	German, English, French, basic Bahasa Malaysia
Teaching	Courses: ”Introductionary Biology” and ”Ant behaviour”

11 Publications

Feldhaar, H. and Stein, J. (1998). Stress proteins and molecular chaperones – protectors of intestinal epithelial damage? *Z Gastroenterol*. 36:193-195.

Feldhaar, H., Fiala, B., Rosli bin Hashim and Maschitz, U. (2000). Maintaining an ant-plant symbiosis: secondary polygyny in the *Macaranga triloba-Crematogaster* sp. association. *Naturwissenschaften* 87: 408-411.

Feldhaar, H., Fiala, B., Gadau, J., Maryati Mohamed and Maschwitz, U. Molecular phylogeny of *Crematogaster* subgenus *Decacrema* ants (Hymenoptera: Formicidae) and the colonization of *Macaranga* (Euphorbiaceae) trees. Submitted.

Feldhaar, H., Fiala, B., Rosli bin Hashim and Maschwitz, U. Dynamics of the *Crematogaster-Macaranga* association: The ant partner makes the difference. Submitted.

Moog, J., Feldhaar, H. and Maschwitz, U. On the caulinary domatia of the SE-Asian ant-plant *Zanthoxylum myriacanthum* Wall. ex Hook. f. (Rutaceae) and the protection against herbivory. Submitted.

12 Contributions to conferences

Feldhaar, H., Rosli, H., Fiala, B. and Maschwitz, U. (2000). Differences in colony-structure of *Macaranga*-inhabiting *Crematogaster* species. 2nd ANet-meeting Kota Kinabalu, Malaysia (Talk).

Feldhaar, H., Fiala, B., Gadau, J. and Maschwitz, U. (2001). Phylogeny of the ants of an ant-plant symbiotic system: the *Crematogaster-Macaranga* association. Proc. VIII Congr. of the European Society for Evolutionay Biology (ESEB), Aarhus, Denmark, p. 319 (Poster).

Feldhaar, H., Fiala, B., Gadau, J. and Maschwitz, U. (2001). Dynamics of the *Crematogaster-Macaranga* association: colony structure of the ant-partner makes the difference. Jahrestagung der Europäischen Sektion der ”International Union for the Study of Social Insects” (IUSSI), Berlin (Talk).

Feldhaar, H., Fiala, B., Gadau, J. and Maschwitz, U. (2002). How life-history traits of the ant partner influence the specificity of the *Crematogaster-Macaranga* association. 15. Jahrestagung der Gesellschaft für Tropenökologie (gtö), Göttingen (Talk).

13 Declaration/ Erklärung

Ich erkläre hiermit an Eides statt, daß ich die vorliegende Dissertation selbständig angefertigt habe und dabei keine anderen als die von mir angegeben Quellen und Hilfsmittel benutzt habe.

Diese Dissertation hat weder in gleicher noch in veränderter Form in einem anderen Prüfungsverfahren vorgelegen.

Ich habe früher außer den mit dem Zulassungsantrag urkundlich vorgelegten Graden keine weiteren akademischen Grade erworben oder zu erwerben versucht.

Würzburg, den 19.05.02

Heike Feldhaar