AN UNUSUAL MYRMECOPHYTIC *MACARANGA* ASSOCIATION, OCCURRING IN A DISJUNCT AREA IN THE MONSOON ZONE OF SOUTH-EAST ASIA: PHENOLOGY AND THE DESCRIPTION OF A NEW ANT SPECIES

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Abstract. The phytogeographic boundary Pattani-Kangar on the Malay Peninsula near the Malay-Thai boundary, between the evergreen rainforest and the Thai semi-evergreen rainforest, is the northern distribution limit of most myrmecophytic *Macaranga* associations. Only three myrmecophytic *Macaranga* species were found to occur along the northern distribution boundary of perhumid conditions: *M. bancana*, *M. hypoleuca* and *M. griffithiana*. We found no uninhabited plants there, suggesting that the distribution ranges of myrmecophytic *Macaranga* species and their associated *Decacrema* ants are largely concordant. *Macaranga griffithiana* was additionally found much further north in a disjunct area in continental eastern Thailand near Cambodia. It is the only myrmecophytic *Macaranga* species known to occur in the seasonally dry monsoon zone, which is possible because of exceptionally high rainfall in the so-called Chantaburi pocket. Here it is associated with a *Camponotus* (*Colobopsis*) species (Formicinae) instead of the typical southern *Crematogaster* (*Decacrema*) (Myrmicinae) partner ants. Also the endophytic trophobiotic scale insect partner differs from the species found in the southern populations. A new ant is described in this paper as *Camponotus markli*, belonging to the *Colobopsis vitreus* species group. This species, which is different from other known *Camponotus* plant-ant partners of *Macaranga*, is a specific partner of its plant, colonizing polydomously several trees and probably defending them against herbivores and climbers. The evolutionary implications of the disjunct distribution of *Macaranga griffithiana* and its partners are discussed. They are hypothesized to be relicts of larger former distribution ranges and of differing ancestor associations in former times. *Accepted 28 April 2004.*

Key words: ant-plants, Camponotus (Colobopsis) markli *sp.n.*, *coccids*, *Chantaburi pocket*, *disjunct distribution*, Macaranga, *myrmecophytic three-partner association, Thailand.*

INTRODUCTION

The most prominent ant-plant system of perhumid South-East Asia consists of the pioneer tree genus *Macaranga* and its manifold associations with ants. The genus *Macaranga* (Euphorbiaceae) comprises species which are not ant-inhabited and/or facultatively ant-associated as well as obligate ant-plants (review in Fiala 1996, Fiala *et al*. 1999). While food bodies and/or extrafloral nectar produced by non-myrmecophytic species attract various opportunistic ants for occasional visits, obligate myrmecophytes also offer nesting space for their specific ant partners. In obligate myrmecophytes, the ants also harvest honeydew pro-

duced by specific scale insect partners maintained inside the internodes (Heckroth *et al.* 1998). In exchange for the provision of food and nesting sites, the ant partners effectively protect their host plants against herbivore damage, competition by climbers (e.g., Fiala *et al*. 1989, Heil *et al*. 2001) and fungal infection (Heil *et al*. 1999). For further details on ecology and biology of ant-associated *Macaranga* we refer to the extensive work of our group in the last 15 years (for overview see, e.g., Fiala & Maschwitz 1990, 1992; Fiala 1996, Fiala *et al*. 1999, Blattner *et al*. 2001, Federle *et al*. 2001, Feldhaar *et al*. 2003a, and references therein).

Macaranga comprises about 280 species with a range stretching from West Africa throughout the Oriental region eastward to the Fiji Islands (Whitmore 1973). It is the only plant genus in the palaeotropics

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exhibiting such a substantial radiation of myrmecophytes (about 29 known myrmecophytic species in the Malayan Archipelago, see recent revision of Davies 2001). Most myrmecophytic species are found in two sections (*Pachystemon* and *Pruinosae*) each of which, although closely related, represents separate evolutionary acquisitions of myrmecophytism (Blattner *et al.* 2001, Davies *et al.* 2001). The majority of partner ants belong to the myrmicine genus *Crematogaster* (subgenus *Decacrema*). Additionally, two *Macaranga* species (*M. puncticulata* and *M. lamellata*) were found to be specifically inhabited by species of the genus *Camponotus*, subfamily Formicinae (Maschwitz *et al.* 1996; Federle *et al.* 1998a, b; Fiala *et al.* 1999).

The center of diversity of this group of three-partner associations (plants, ants and scale insects) is Borneo, spreading westward to Sumatra and northward to the Malay Peninsula (Fiala *et al.* 1999), with Borneo hosting many more endemic host plant species (see revision of Davies 2001) and more ant lineages as well (Fiala *et al.* 1999, Feldhaar *et al.* 2003b). So far no information exists on the age and geographic origin of the *Macaranga*-ant system. The first (non-myrmecophytic) *Macaranga* species – thought to be bushlike pioneers of open places – was hypothesized to originate in the Oligocene or early Miocene (38 to 15 mya) when the climate was predominantly seasonal and dry (Slik & 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) and also when the greatest northward extension of rainforest occurred, so we assume a development of the first close *Macaranga*-ant associations not before this period. For any interpretation of the evolutionary development of the *Macaranga*-ant associations, information on their biogeography is required. The section *Pachystemon*, which comprises most myrmecophytic species, is restricted to the moist tropics within the floristic boundaries of West Malesia (*sensu* van Steenis 1950) and does not extend into the more seasonal monsoon forest regions (e.g., Whitmore 1975, Fiala *et al.* 1999, Davies 2001). We do not know what limits the distribution of the myrmecophytic associations. Climatic factors certainly play an important role since low temperature and increased dry periods do not allow continuous food production of the plants for their partner ants. Inhabited myrmecophytic trees in the Malay Archipelago do not occur above 1250–1400 m (Fiala *et al.* 1999), although ants not associated with myrmecophytes were still found foraging

on vegetation up to 2300 m in the Mt. Kinabalu area, Sabah (Kern 1996). Since ants and plants as well as associated coccids are usually not able to survive without each other (e.g., Fiala 1996, Heckroth *et al.* 1998), and ants were never found outside their host plants, it is difficult to tell whether *Decacrema* ants alone could survive in other climatic zones. The interdependency of all partners is so strong that obviously their distribution range is always correlated. Here we add data on the northern border of the distribution of the *Macaranga*-ant system in the perhumid zone. In addition, we describe in more detail an unusual association isolated in the monsoon zone of continental Thailand. The plant partner of this association, *Macaranga griffithiana* Müll.Arg. (nomenclature following the revision of Davies 2001), was already known from Peninsular Malaysia and Sumatra as an obligate myrmecophyte associated with a *Decacrema* ant-partner (Fiala *et al.* 1999, therein named *Macaranga motleyana* ssp. *griffithiana* (Müll.Arg.) Whitmore since it was formerly considered as a subspecies by Whitmore 1974). *Macaranga griffithiana* has also been collected from Indochina (reported in Davies 2001): from Laos (1 specimen from Bassin du Se Moun), Vietnam (3 specimens, with site records: Cochinchine, Saigon and Annam) and from Cambodia (H. Sovanly, pers. comm.). No information, however, exists concerning its possible ant-inhabitation there. For the two existing herbarium specimens in the Museum of Natural History in Paris, no information was provided by the collectors (Poilane 22164 Vietnam, and Martin 1000 Cambodia) about the presence of associated ants nor are there obvious ant exit holes in the twigs of these specimens (S. Hul, pers. comm.). *Macaranga griffithiana* is the only species of section *Pachystemon*, in fact even the only myrmecophytic *Macaranga* species known from southeast Thailand – rather far outside the usual distribution range – which makes it especially interesting with regard to evolution of host use in this system. *Macaranga griffithiana* in southeast Thailand was found to be ant-colonized, however, not by *Decacrema* species but by a taxonomically completely different ant, which was associated with a little-specialized coccid partner. This ant turned out to be a new species and will be described in this paper.

MATERIAL AND METHODS

In the years 1990, 1999 and 2001 we performed three excursions in search of myrmecophytic *Macaranga* species at the distribution boundary: along the Thai
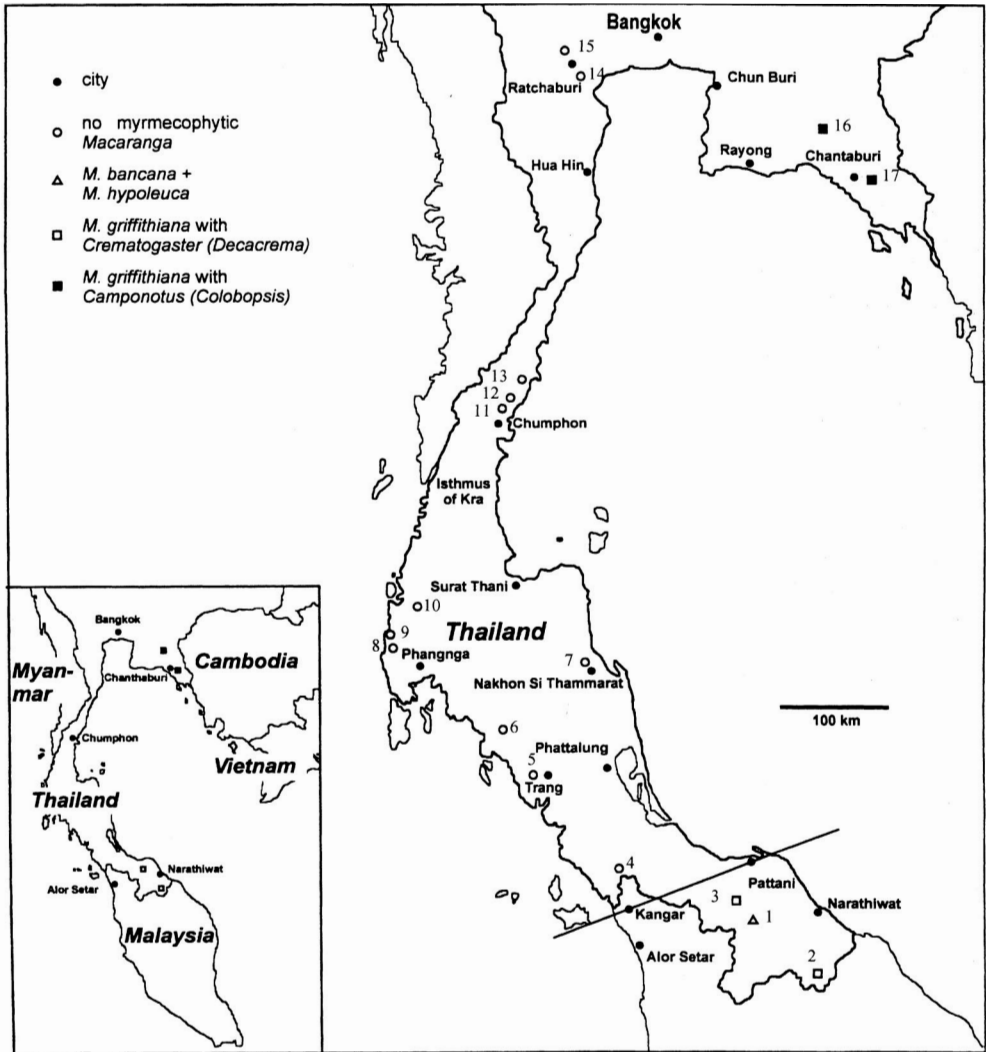
FIG. 1: Distribution map of different *Macaranga* species at study sites investigated in Peninsular Malaysia and Thailand.

border in northern peninsular Malaysia and southern peninsular Thailand, in the area near Ratchaburi and in the northeastern gulf coastal region in the areas of Pattaya, Rayong and Chantaburi. As most of the easily accessible areas are cultivated, we searched mainly near national parks in and around which some natural vegetation remains. The plants (mainly saplings) were surveyed in the field and the partner insects were collected in ethanol and identified. Due to time restrictions and logistical problems we were not able to perform any experiments with the partner ants.

RESULTS

Habitat and geographic distribution of myrmecophytic *Macaranga* species

Southern habitats and distribution range. Only three myrmecophytic *Macaranga* species (all section *Pachystemon*) were found to occur along the northern distribution boundary of the myrmecophytic associations: *M. bancana*, *M. hypoleuca* and *M. griffithiana*. We found no uninhabited plants, suggesting that both partners do not occur separately and that the distribution range of the associated *Decacrema* closely matches that of the respective host plants.

Macaranga bancana and *M. hypoleuca* were localized in southern Thailand near Yala south of the Pattani-Kangar borderline (Fig. 1(1)), where they were found on a hill at 250–800 m. No more of these plants were found by us in suitable habitats in the hills of Khao Sok (Fig. 1, (10)), Khao Lak Lamru (west coast, (9)) and Khao Phanom Thale Ban N.P. (west coast, (8)), as well as in the Khao Luang N.P. (east coast, (7)). Already on Gunung Jerai (in Kedah/Malaysia near Sungai Patani) these plants were not found below 150 m but did grow in higher regions up to 900 m. *Macaranga bancana* was inhabited by its typical *Decacrema* partner ants (morphospecies (msp.) 4, nomenclature after Fiala *et al.* 1999), and *M. hypoleuca* was found with msp. 1.

M. griffithiana in Peninsula Malaysia is a very common lowland ant-plant found mainly in open disturbed habitats with moist to swampy soils, i.e. on plains which can be flooded during wet times, on banks of streams, etc.. Roadside drains are frequently occupied by *M. griffithiana*. It was usually associated with *Crematogaster* (*Decacrema*) msp. 1 and with a specific coccid partner (*Coccus caviramicolus*) although a few other scale species also occurred.

In perhumid southern parts of peninsular Thailand we localized the plant and its typical *Crematogaster* partners in road drains close to the Thai-Malaysian border in the lowland east coast area near Sungai Ko Lok (see map, Fig. 1(2)). The next location further northward was also an east coast lowland location 30 km south-southwest of Pattani (Fig. 1 (3) on the swampy banks of a small slowly flowing stream between rubber plantations. In the six accessible rather small plants, *Decacrema* msp.1 was found but no coccids. From here northward we checked a great number of similar lowland habitats (all following numbers after localities, refer to Fig. 1) both on the east and west side of the peninsula, especially south but also north to the Isthmus of Kra, known as the boundary between perhumid and monsoon climate.

South of the Isthmus of Kra (but north of the phytogeographic Pattani-Kangar borderline between the evergreen lowland forest to the semi-evergreen rainforest, Whitmore 1984) we surveyed swampy lowland parts of various national parks (Thale Ban N.P. (west coast, (4)), Thang Tieo N.P. ((6), near Khlong Phon), Khao Sok (10) and Khao Lak Lamru (9)). These in part looked highly suitable for the occurrence of *M. griffithiana* but nevertheless the plant could be localized nowhere. Also in the swampy area around Thung Kai Botanical Garden near Trang ((5), with a protected central peat-swamp forest) and in a well developed freshwater swamp with large *Pandanus* trees near Thap Lamu (west of (10) Ban Haouy Mai Pai, west coast) no *M. griffithiana* plants could be found. Similar, on the peninsula north of the Isthmus of Kra (north of Chumphon) several disturbed swampy sites were checked without success, as well as the Bang Sa Ban Yai forest (11-13). No *M. griffithiana* plants were found in Central Thailand ca. 100 km west of Bangkok in six suitable swampy habitats checked along river banks (14, 15).

In south-east Thailand 160 km south-east of Bangkok, about 80 km from the Cambodian border, we finally found *M. griffithiana*, associated, however, with a different ant species: a *Camponotus* sp. from the subfamiliy Formicinae.

The ant-association of *Macaranga griffithiana* in NE Thailand

Habitats. We found two large dense and well ant-populated *M. griffithiana* tree populations, one at several sites in the Khao Chamao National Park (16) near Klaeng and Rayong (n > 50), and another near the Khao Sa Bap National Park (17) in the vicinity of Chantaburi (n > 100). Its habitats – namely freshwater swamp – strongly resembled those of the west Malaysian *M. griffithiana*–*Crematogaster* (*Decacrema*) associations. We found them in dense populations on non-flooded, forested flat banks of slowly moving streams. All those habitats were rather disturbed. In the dry season during our study period (January–February), they were located just behind the permanently wet area. In densely forested parts of the habitat the trees grew taller, whereas they were more shrublike in open habitat parts.

A third small isolated population in a heavily disturbed swampy area about 50 km east of Chantaburi along the highway consisted of small treelets (n = 30). Only three ant-colonized trees could be discovered

here, one tree of about 3 m in height with a large ant colony and 2 saplings (1–1.2 m) with only colony-founding queens. All plants in the population showed heavy herbivore damage and were covered with vines, except for the tree with the ant colony. This population is not further treated in this survey. Along the highway three isolated plants were found scattered along the roadside, most of them uninhabited. Other *Macaranga* species in this area were the widespread *M. tanarius* as well as *M. denticulata* and the recently described *M. siamensis* (Davies 2001), all non-myrmecophytes.

Plant characters. *M. griffithiana* grew up to 15 m within forested habitats but was most common as a bushy treelet or broadly ramified shrub at open sites and forest edges. Thin young stem parts and branches, as well the undersides of the rather weakly trilobed leaves, are waxy and whitish in color. The stem becomes hollow by pith degeneration thus forming internodal domatia. Seedlings can begin to develop domatia at a height of less than 0.5 m; below that height stems often still have a rather small diameter (about 5 mm only).

The paired stipules are rather short lived and persist only in the two or three most apical leaves of a shoot. Food bodies are found beneath the stipules and (as seen on saplings kept in the greenhouse) in large numbers on both sides of young leaves, preferably close to the veins.

Distinct morphological differences between the main southern populations and the disjunct northern population around Chantaburi could not be recognized. Slight differences in the shape of the stipules were found in plants from Chantaburi and Pattani (both flat-shaped) and in plants growing ca. 400 km further south (bowl-shaped).

Ants. Whereas the southern population of *M. griffithiana* in the perhumid zone of the Malay Peninsula was inhabited by *Crematogaster* (*Decacrema*) msp. 1, the disjunct northern population was associated with a black dimorphic *Camponotus* (*Colobopsis*) not belonging to the *cylindricus* species groups (as the partner ant of *Macaranga puncticulata*, Federle *et al.* 1998 a,b) and described below as *Camponotus* (*Colobopsis*) *markli* n. sp. In three different separate subpopulations altogether 87 trees and treelets, including resprouts from cuttings, were checked in more detail. Of 29 young plants (0.5 to 2 m) only 21% were associated with *Camponotus* (*Colobopsis*) *markli* n. sp.

although they already possessed swollen hollow stems. Of 58 larger plants (2 m to > 20 m), 81% were inhabited by *C.* (*Colobopsis*) *markli*. We found other ants only in 3 trees, one with an unidentified arboreal *Crematogaster* sp. (non-*Decacrema*) and two with a different *Camponotus* (*Colobopsis*) species than the apparently *Macaranga*-specific *C.* (*Colobopsis*) *markli* (one of them together with a small colony of *C.* (*Colobopsis*) *markli*). *Camponotus* (*Colobopsis*) *markli* could also be observed in two other small subpopulations of *M. griffithiana*. On more than 120 trees other than *M. griffithiana* checked in the close vicinity of the collection sites *C. markli* was not found.

Coccids. In all three populations most colonies were found to be associated with one coccid species in varying numbers, which could be identified as *Coccus* morphospecies 214 (Heckroth *et al.* 1998). One small subpopulation with about 10 *C.* (*Colobopsis*) *markli* colonies contained no coccids. Nevertheless, colonies here were also well developed and contained brood.

Colony structure, ant behavior and plant-ant characters

During our survey of *M. griffithiana* saplings we never found a *Camponotus* (*Colobopsis*) *markli* colony with more than one queen, possibly indicating monogyny in this species. We did not, however, dissect whole trees with large colonies. The nodal regions of the stems and branches were mostly hollowed out by the ants. Thus a widely uninterrupted passage through the plant resulted. The round entrance holes in the internodes looked very regular, were obviously bitten by the ants and had a diameter of 1–2.5 mm (average $\bar{x}$ = 1.69 ± 0.31 SD, n = 15). They were partly closed by callus growth in the lower parts of the tree.

Similar to the *Colobopsis* sp. association with *M. puncticulata* (Federle *et al.* 1998a, b), larger colonies often apparently occupied several trees. This was indicated by the fact that no fertile queens could be found in smaller trees close to larger ones with a physogastric queen. One such cluster consisting of seven trees between 3.5 and 6.5 m in height, growing in a rectangle of 2.5 m², was thoroughly checked for its ant inhabitants in more detail: only in one central tree, 5.5 m in height, did we find a strongly physogastric queen in the stem interior about 3 m up. All trees contained ant brood (including the cocoonless pupae), adult ant workers, soldiers, many alate young queens, and in one tree two males.

The workers were observed to patrol on the tree and collect food bodies. In larger colonies the work-

ers attacked human disturbers by biting, but not in a very aggressive way. Though we have not observed pruning behavior directly, *C.* (*Colobopsis*) *markli* very likely shows this behavior. As typical for pruning plants, well colonized trees were free from vines as a rule, whereas uncolonized trees often were more or less covered by vines. In four well accessible trees at the forest edge we observed freshly destroyed (with biting marks) shoots of *Mikania* sp. (Asteraceae), a fast growing non-woody climber, which occurred at such sites on well exposed bushes and trees in the surroundings. This climber was also abundant nearby on bushy *M. griffithiana* without ant inhabitants.

Colony foundation of C. (*Colobopsis*) *markli* n. sp. We discovered only five colony founding-queens in saplings of between 1.8 and 2.5 m in height. These foundation colonies, however, looked very similar to those of other typical specialized plant ants in the *Macaranga* system. Foundation appeared to occur claustrally, with the queen biting an entrance hole into an internode which afterwards closed. Two young queens were found with brood but were still workerless. The round entrance holes of the still claustral queens had begun to close by growth but still contained remains of a carton closure material. Three queens were with a few small workers which had bitten a small hole near an old larger entrance hole, apparently formerly bitten by the queen and subsequently closed by plant growth. All five foundation chambers contained no scale insects, indicating that the young scales likely arrived as crawlers by wind transport as in the *Macaranga–Crematogaster* associations (Heckroth *et al.* 1998) and that the large queens raise their first offspring using their own body reserves without the help of any trophobionts.

DISCUSSION

Macaranga-ant associations at the edge of their distribution in peninsular Thailand. All populations of the *Macaranga* species section *Pachystemon* (*M. griffithiana*, *M. bancana* and *M. hypoleuca*) found by us in peninsular Thailand always occurred together with *Decacrema* partners, i.e. these associations are retained up to the distribution boundary, indicating that they are in any case strictly obligate and specific. Clearly *Macaranga* plants can nowhere occur without their ant partners. This is probably due to their own weak defense abilities against herbivores, apparently reduced

during their myrmecophytic evolution. The defense is taken over by their ant partners (e.g., Fiala *et al.* 1989, Eck *et al.* 2001, Heil *et al.* 2001). *Macaranga bancana* was found with its main ant partner msp. 4, while *M. hypoleuca* was found with msp. 1. This is in contrast to southern regions on the Malay Peninsula where *M. hypoleuca* is mainly colonized by msp. 6 as a sapling and msp. 1 occurs usually as a secondary colonizer in larger trees (Fiala *et al.* 1999, Feldhaar *et al.* 2003a). When saplings of *M. hypoleuca* in peninsular Malaysia were found to be colonized by msp. 1, this occurred most often in rather disturbed habitats (Fiala *et al.* 1999). So the shift from msp. 6 to msp. 1 further north could indicate changing climatic and/or anthropogenic environmental conditions, which may reduce the dispersal or competitive ability of msp. 6. Morphospecies 1 inhabits several host plants from different clades of the section *Pachystemon*, as well as section *Pruinosae*. It therefore has the broadest host-plant range of all *Decacrema* but occurs as first colonizer of small saplings mainly in *M. griffithiana* and *M. pruinosa*. Despite being a specific *Macaranga* partner, msp. 1 has been shown to be a less effective defender than other *Decacrema* species (Fiala *et al.* 1990 and unpubl. observations, Federle *et al.* 2002).

All myrmecophytic *Macaranga* populations found by us in peninsular Thailand were localized far south of the monsoon borderline on the Isthmus of Kra at about 10° N south of a floristic distribution line across the peninsula reaching from Pattani to Kangar (Fig. 1). This line represents a border between the evergreen Malay rainforest and the Thai semi-evergreen rainforest (Whitmore 1984). On its evergreen forest side, e.g., Red Meranti-type *Shorea* species are found as well as moisture-demanding underground arecoid palms, which are lacking further north. However, most forest in the lowlands has been lost to agriculture. Whether *M. bancana* and *M. hypoleuca* are in fact found northward of the Isthmus of Kra in lower Myanmar (Airy-Shaw 1972) has to be reconfirmed. From this region (west-facing slopes of the Tenasserim Hills), which is wetter than the Thai side, some regional evergreen areas are reported in the extreme south (Whitmore 1984). No information exists on ant-association. A literature search also revealed no herbarium records from further north than our own findings, which was also the case for the remaining myrmecophytic species occurring in peninsular Malaysia (*M. hosei, M. hullettii, M. kingii, M. pruinosa, M. puncticulata*).

The northern disjunct population of Macaranga griffithiana and its partners. Macaranga griffithiana is the only myrmecophytic *Macaranga* species which occurs in the seasonally dry monsoon zone. The few sites where it can be found in eastern Thailand also contains other plant species usually restricted to the peninsular perhumid zone, e.g., *Dyospyros hermaphroditica* and several bamboo and understory palms. This was stressed by Whitmore (1984 and pers. comm.), who coined the term "Chantaburi pocket" for this area. Apparently some climatic differences exist here compared with the surrounding areas due to the rain relief area of the wet western slopes of the Cardamon mountains. It is reported to receive exceptionally high rainfall for this region (> 3000 mm/year; source: online data of Thailand Royal Irrigation Department). Here a complex vegetation mosaic exists due to the locally variable rainfall and soil conditions. The preference of *M. griffithiana* for very swampy soils obviously adds to its survival in the dry seasons. At present, it must remain open whether the *M. griffithiana/ Camponotus symbiosis* extends further eastwards into Indochina. There are no published records and all our enquiries with local botanists in Cambodia and Vietnam have so far revealed no information about ant association in these regions.

In the perhumid zone of the Malay Peninsula the specific partners of *M. griffithiana* are mainly *Cremaptogaster* (*Decacrema*) msp. 1 and along the east coast also msp. 5 (Fiala *et al.* 1999). The dominant specific scale insect partner was *Coccus caviramicolus*, which was rather rare on other *Macaranga* species.

In the disjunct "Chantaburi" *M. griffithiana* populations we found no *Decacrema* ants but the plants were exclusively colonized by *Camponotus* (*Colobopsis*) *markli*. This is again a different species than the other two myrmecophytic *Camponotus* species so far found in *Macaranga, C. macarangae* living in *M. lamellata* (Maschwitz *et al.* 1996) and *C.* (*Colobopsis*) sp. (belonging to the *cylindricus* species group) in *M. puncticulata* (Federle *et al.* 1998 a,b).

Queens of *C.* (*Colobopsis*) *markli* were found in the upper third of the trees. This is as in *Camponotus macarangae*, but in contrast to primary colony foundations of *Crematogaster* (*Decacrema*) in other *Macaranga* species where the first colony-founding queens remain in lower parts of the stem. However, we have also found colonizing queens of *Crematogaster* (*Decacrema*) msp. 1 in *Macaranga griffithiana* in higher stem parts than in other *Macaranga* species (as high as 1.5 m) perhaps due to the fact that the stem dia-

meter often remains rather small up to a sapling size of about 0.5–0.7 m. In addition, the plants grow in swamps and lower stem parts might become subject to flooding in the rainy season. One can also not rule out the possibility that we have to deal with a succession of different colonizing queens during the ontogeny of the plant. We found taller trees of *M. griffithiana* in Peninsula Malaysia that were newly colonized by *Decacrema* msp. 1 queens which were then located in the branches of the tree and not in the trunk (Feldhaar *et al.* 2003a). Such a colonization of the crown region might also occur with *Camponotus* (*Colobopsis*) *markli.*

Camponotus (*Colobopsis*) *markli* was found to be associated with one scale insect species, *Coccus* msp. 214. This species was already known from various *Macaranga*-ant associations, also from *M. motleyana*, the sister species of *M. griffithiana* in Borneo. It is a rather polyphagous endophytic scale insect which was, in contrast to most coccids collected from *Macaranga*, also rarely (n = 7) found in other hollow plants, such as *Myrmeconauclea*, and even in non-myrmecophytic lianas like *Uncaria*, and was tended by unspecific arboreal *Crematogaster* ants (Heckroth *et al.* 1998).

Crematogaster macarangae living in *M. lamellata* (Borneo) was associated with typical specific coccids also found in *Decacrema* associations but not with *Coccus* msp. 214. *Camponotus* (*Colobopsis*) sp. with *M. puncticulata*, however, forms a two-partner system where no trophobionts are tended and the ants live on nectar and food bodies provided by the plants (Federle *et al.* 1998 a,b).

The degree of ant-colonization was locally rather low, which was also the case in *C.* (*Colobopsis*)-*M. puncticulata* associations. At two sites we found destroyed or partly destroyed colonies, the domatia of which were torn open in a similar way as observed in various *Macaranga* species in Peninsular Malaysia and in Borneo. There, mainly squirrels were identified as the destroyers (Federle *et al.* 1999) but also birds were observed (B. Fiala, pers. observation). A further reason, however, might be the very disturbed and fragmented habitat. Extensive open areas might limit the dispersal of the colonizing queens (Fiala *et al.* 1999).

Nevertheless, several characters of the association partners are characteristic of close myrmecophytic relationships:

– maintenance of the full set of ant-plant characters in *M. griffithiana*, i.e., formation of thin-walled, fragile domatia, and a high rate of food body production,

– the high specificity of associations at several separated subpopulations in open and in forested habitats, monopolization of trees by colonizing ants although other arboreal ant species were present,

– host plant localization, and domatium opening behavior (chewing of entrance holes into living plant tissue) of the colony-founding queen,

– frequent food body consumption by the partner ant,

– aggressiveness and probable pruning behavior (this was also reported from *C.* (*Colobopsis*) colonizing *M. puncticulata*, Federle *et al.* 1998a),

– presence of a single coccid partner species. This homopteran tending as well as food body harvesting can make the ants independent of food searching away from the plant.

All these characters taken together speak for a close association of all three partners. It obviously represents another example of the independent origin of a myrmecophytic association within the diverse genus *Macaranga*. The two other associations of *Macaranga* plants with *Camponotus* species differ in many aspects to the one reported in this study. The *Macaranga* species involved are not closely related, *M. griffithiana* (West Malaysia, Thailand) and *M. lamellata* (Borneo) belong to different clades within the section *Pachystemon*, and *M. puncticulata* (West Malaysia) is even more distant, forming an own clade (Blattner *et al.* 2001, Davies 2001). On the ant side as well, initial phylogenetic analyses based on mitochondrial DNA sequence data of all *Camponotus* species involved revealed that *C.* (*Colobopsis*) *markli* is not closely related to either of the other *Macaranga*-colonizing *Camponotus* species (J. Gadau *et al.*, unpubl. results), i.e., has obviously evolved independently as a plant-ant.

Macaranga-associated *Decacrema* species have not yet been found outside their host plants, not even on other myrmecophytic plants in the region, which suggests a close coevolution between ant and plant. However, our phylogenetic analysis (Feldhaar *et al.* 2003b) and host association studies (Fiala *et al.* 1999) do not indicate strict cocladogenesis because *Decacrema* ant species occur on quite distinct host-plants belonging to different clades within the genus *Macaranga*. Findings from this and other studies (for an overview see Fiala *et al.* 1999) that even ants from other subfamilies occur as *Macaranga*-ant partners make a strict general cocladogenesis, as proposed by

Itino *et al.* (2001), more unlikely. We assume that host-shifting or host-expansion is common in the ants colonizing *Macaranga*.

Possible historical reasons for the disjunct occurrence of Macaranga griffithiana and its differing association partners. Corresponding to its high diversity, the evolutive origin of the *Macaranga*-ant complex probably lies far to the south in the center of Sundaland. The section *Pachystemon* to which *M. griffithiana* belongs can be divided into four clades (revision Davies 2001, Bänfer *et al.*, in press). ITS sequences are highly similar within the section *Pachystemon*, suggesting a relatively recent and rapid radiation of obligate myrmecophytes within this section. Clade 2 with *M. griffithiana* forms a well supported sister group (Blattner *et al.* 2001) to clade 1, which contains most myrmecophytic species. *Macaranga griffithiana* also has a distinct pollinator: whereas most *Pachystemon* are visited by thrips of the genus *Neoheegeria* (Phlaeothripinae), *M. griffithiana* was mainly found with the genus *Thrips* (Thripinae) (Moog *et al.* 2002). However, *M. griffithiana* has no isolated position within the section and it is very closely related to the Bornean endemic *M. motleyana*, thus not suggesting a lengthy separate evolution. Our first results on chloroplast DNA sequence variation indicate that myrmecophytism possibly evolved on Borneo. The distributions of haplotypes, however, correlated with geographically circumscribed regions rather than taxonomic boundaries and haplotypes of *M. griffithiana* from SE Thailand, were clearly distinct (Moog *et al.*, unpublished results).

According to our results (e.g., Fiala *et al.* 1989, Fiala *et al.* 1999, Heil *et al.* 2001) obligate myrmecophytic *Macaranga* species are fully dependent on their partner ants and do not reach maturity without them. As all known ant-plants, including *M. griffithiana*, are obligate myrmecophytes, a successful dispersal of the plant partner over long distances is possible, but successful reproduction of isolated plants without their ant-partners becomes very unlikely, thus limiting the migration opportunities of such a system. This effect will be enhanced by the dioecious mating system of *Macaranga*, which needs at least two successful seed dispersal events to colonize a certain area. Thus myrmecophytic *Macaranga* species should only rarely be able to establish new populations in areas remote from already existing ones. We therefore believe it more likely that the *M. griffithiana*-ant asso-

ciation already existed in this northern continental area during a time of habitat enlargement in a moister climatic period.

South-East Asia was effectively a single land mass and the region remained as a single rainforest block until the late Miocene-early Pliocene (Morley 2000). With the advent of Quaternary glaciations repeated fragmentation of rainforest sites occurred, leading to isolation and possible further speciation events. Landbridges between Borneo and peninsular Malaysia probably existed until as recently as 10 000 years ago, enabling exchange of floral and faunal elements (for details see Voris 2000). Also the large rivers draining the Sunda shelf probably provided forest refugia along their banks.

Two scenarios can be imagined:

a) *Camponotus* (*Colobopsis*) *markli* n.sp. was the regular ant partner of the ancestor plant species of the symbiosis. It occurred throughout the whole range, together with a rather unspecific scale insect directly related to or identical with *Coccus* morphospecies 214. Due to climatic changes the northern subpopulation persisted only in the moist region of the "Chantaburi pocket", dying out over a long distance further southward. In its main southern perhumid habitat a *Decacrema* ancestor species subsequently took over the ancestral *Pachystemon* precursors of the whole complex. To postulate the Chantaburi association as representing a persistent part of the ancient stock of the whole complex therefore seems to be rather plausible. Davidson & McKey (1993) have proposed the hypothesis that in the course of evolution competitively dominant ant species (e.g., *Crematogaster*) have replaced prior less aggressive ant associates such as *Camponotus*. We have discussed this scenario in detail for the association in *M. lamellata*, where *Camponotus macarangae* occurs sympatrically with a *Crematogaster* (*Decacrema*) partner ant (Maschwitz *et al.* 1996). However, rather aggressive *Camponotus* plant-ants also occur in SE Asia where they exclusively inhabit rattan palms. Most of these very specialized ants belong to the distinct subgenus *Myrmoplatys* Forel (M. Werner, unpubl. results).

b) The second scenario would also imply an isolation from the ancient population. However, the original *Crematogaster* (*Decacrema*) species became extinct in the northern climatic zone perhaps during the increasingly dry and cool climate in the Quaternary. The more aggressive *Crematogaster* are believed to require a greater energy input, so they are not likely to survive in less productive habitats or under conditions of seasonally low resource supply (Davidson & McKey 1993). Therefore an ancestor of *Camponotus* (*Colobopsis*) *markli* was able to take over the empty niche. The ant partner of *M. griffithiana* in southern regions, *Decacrema* msp. 1, belongs to the *captiosa*-group, which shows the most derived characters. Our phylogenetic analysis of the ants (Feldhaar *et al.* 2003b) revealed that msp. 1 and msp. 4 in peninsular Malaysia are morphologically and genetically close, suggesting a rather recent split, therefore making an ancient association with *Decacrema* msp. 1 less likely. However, given our current state of knowledge, a decision in favor of one of these scenarios is not possible. It is also not possible to decide whether the recent main *Coccus* partner of the southern *M. griffithiana*, *C. caviramicolus*, a) never came into contact with the disjunct association, or b) got lost during isolation and was replaced by the more generalistic and widespread *Coccus* msp. 214. Investigations on competitive abilities of *Crematogaster* and *Camponotus* and further phylogenetic studies on ants, plants and scale insects will help to clarify these questions.

DESCRIPTION OF THE ANT SPECIES

(K. Dumpert)

The ant species belongs to *Colobopsis*, which is a subgenus of *Camponotus* (Emery 1925). This subgenus is characterized by having the anterior portion of the head sharply truncated in the soldier and queen castes. They are used to block the entrances to the arboreal nests inhabited by these ants (e.g., Szabó-Patay 1928). To some extent truncated heads are also found in the *Camponotus* subgenera *Hypercolobopsis* Emery, *Pseudocolobopsis* Emery and *Myrmamblys* Forel, which show a morphological trend toward phragmosis, in the form of partial or complete truncation of the anterior end of the head. While *Hypercolobopsis* and *Pseudocolobopsis* are known from the American continent only, there are many species of *Myrmamblys* known from Africa, Asia and Australia. The new species we found living in *Macaranga griffithiana* does not belong to this subgenus. Difference: Antennal insertion not near the front end of the midlength of the frontal carinae but more or less near the midlength (like *Colobopsis*).

According to Emery (1925), the subgenus *Colobopsis* is divided into the following 6 groups: *truncatus*, *cottesi*, *conicus*, *dentatus*, *vitreus*, and *cylindricus*. The ant species in question belongs not to *truncatus* be-

cause the phragmotic parts of the soldier and queen heads are not marginated. They also do not belong to the group *cottesi* because the phragmotic parts of the soldier and queen heads are not grossly punctated. The group *conicus* can be excluded because the epinotum is only slightly compressed and not forming a tip at its rear end. Also the groups *dentatus* and *cylindricus* can be excluded because our ant species has no dentated epinotum, as do the members of the group *dentatus*, and no intermediate forms between soldier and worker caste as can be found in the group *cylindricus*.

We conclude that the ant partner of *Macaranga griffithiana* belongs to the *Colobopsis* group *vitreus*. Common characteristics: no intermediate forms between soldier and worker caste, phragmotic parts of the soldier and queens heads are not marginated, all anterior parts of the bodies of all castes are not grossly punctated.

Hitherto known species of *Colobopsis* (*vitreus*) are: *C. gasseri* Forel 1894 from Australia, *C. hosei* Forel 1911 from Borneo, and *C. vitreus* S. Smith 1861 from Malaysia.

According to the original description by Forel – who only described workers and no soldiers and sexuals of this species – and syntypes from the Forel collection, *C. hosei* workers differ from those of *C. markli* in head shape, shape of the tibiae, pilosity and color. The head of *C. hosei* is as long as wide and the sides of the head are convex. In *C. markli* the heads are longer than wide and the sides are straight. The scapal length of *C. hosei* is distinctly shorter than in *C. markli*. The tibiae of *C. hosei* are cylindrical, in *C. markli* not. Pilosity of *C. hosei* decumbent, extremely short and yellowish. This contrasts to the pilosity of *C. markli* that is long, erect and white. Color of *C. hosei* is dark brown, excluding antennae and legs; in *C. markli* the whole body – including legs and antennae – is blackish brown.

Concerning *C. gasseri* we were also able to compare *C. markli* with the original description by Forel and syntypes of the Forel collection. Females of *C. gasseri* differ from *C. markli* females in several characteristics: occipital margin in full-face view straight, ocelli extremely small, petiolar scale in dorsal view rounded, color black except two broad yellow stripes on gaster; head not shining, rest of the body much more opaque than shining. Unlike *C. markli*, *C. gasseri* soldiers and workers are opaque on whole body surface; head

of the *C. gasseri* soldiers distinctly striated especially between the frontal carinae.

The original description of *C. vitreus* was based on the worker caste only. In this species, the original description by Smith (1861) and determined specimens from the Forel collection were at our disposal. Different from *C. markli* are the following characteristics: occipital margin straight, head not elongated but as long as wide, whole animals are much longer and broader than workers of *C. markli*.

Besides material of *C. vitreus* we were also able to examine determined specimens of the subspecies *C. vitreus angustatus* Mayr from the Forel collection. This subspecies from Indonesia is distinctly smaller than *C. vitreus*. But also in this case, occipital margin is straight, head not elongated and pronotum distinctly broader than in *C. markli*. Besides, the color of *C. vitreus angustatus* is brown – instead of blackish brown as in the case of *C. markli*.

Material examined: 5 major and 7 minor workers, 6 females (3 alates and 3 dealate active queens) and 2 males from eastern Thailand.

Measurements and Indices:

Total Length (TL):
The total outstretched length of the individual, from the anterior clypeal margin to the gastral apex.

Head Length (HL):
The straight-line length of the head in perfect full-face view, measured from the mid-point of the anterior clypeal margin to the mid-point of the occipital margin.

HL of soldiers (HLS):
The straight-line length of the head in perfect full-face view, measured from the mid-point of the posterior phragmotic head part to the mid-point of the occipital margin.

Head Width (HW):
The maximum width of the head measured below the eyes in full-face view.

Cephalic Index (CI):
HW x 100 / HL

Scape Length (SL):
The straight-line length of the antennal scape, excluding the basal condyle and neck.
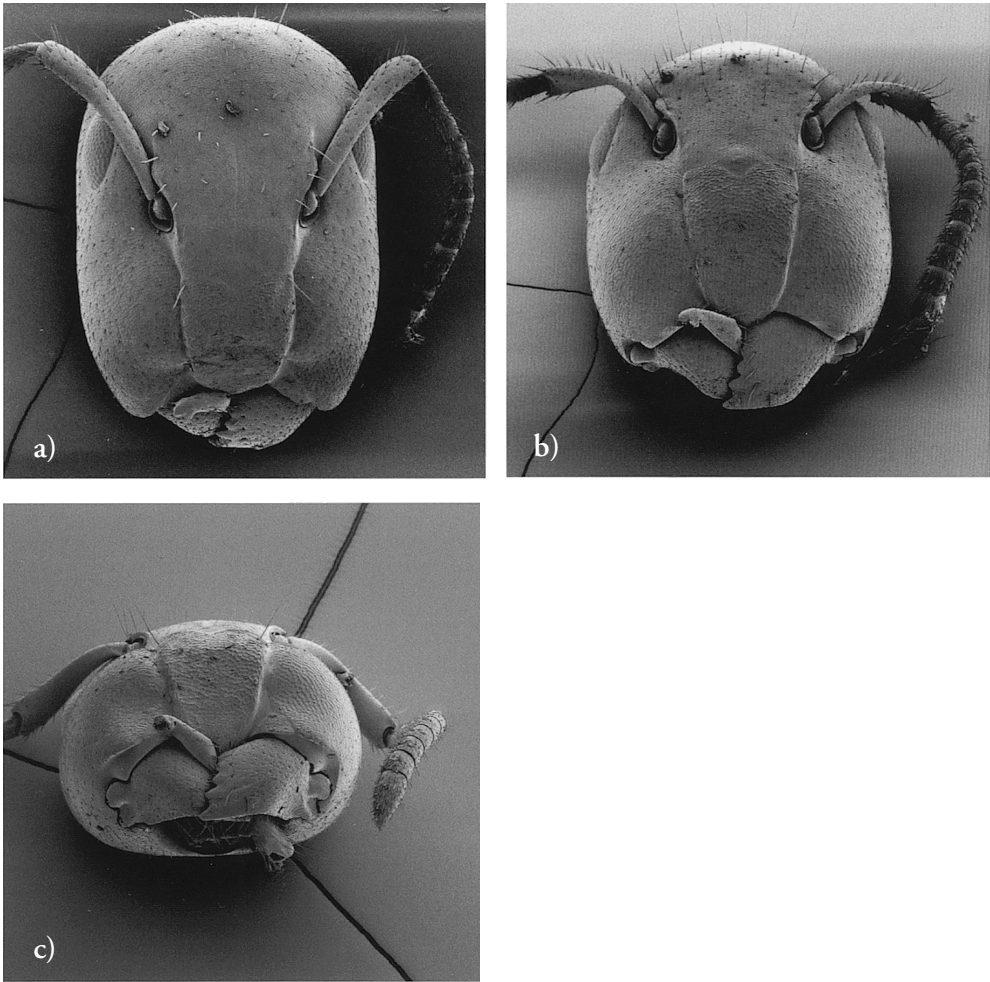
Scape Index (SI):
SL x 100 / HW

FIG. 2: Scanning electron micrographs of *Camponotus* (*Colobopsis*) *markli* soldiers, a) head, b) phragmotic part of the head, c) head, seen from below.

Ocular Diameter (OD):
Maximal diameter of the compound eye.

Ocellar Distance 1 (OD1):
The straight-line length of the distance between the lateral ocelli measured from their inner margin.

Ocellar Distance 2 (OD2):
The straight-line length of the distance between one lateral to the medial ocellus measured from their inner margin.

Ocellar Width (OW):
Maximal width of the medial ocellus.

Pronotal Width (PW):
The maximum width of the pronotum measured in dorsal view.

Petiole Height (PH):
The height of the petiole from the base to the uppermost point.

Petiole Width (PB):

The maximum width of the petiole in dorsal view.

Wing Length (WL):

The outstretched length of the forewing (FWL) and the hind wing (HWL).

Wing Width (WW):

The maximum width of the forewing (FWW) and the hind wing (HWW).

All measurements are expressed in millimetres. They were taken at 40x power with a Leica MZ6 dissecting microscope, using a Leica micrometer. Scanning electron micrographs were taken by means of a Hitachi S 500.

Camponotus (*Colobopsis*) *markli* sp.n.

Derivatio nominis: the species name is dedicated to the great biologist, myrmecologist and president of the Max-Planck-Gesellschaft Prof. Dr. Hubert Markl.

Major workers:

Diagnosis: Distinctly larger than minor workers with respect to TL and the size of the head; no intermediates; distinctly phragmotic; all body parts – including the phragmotic part – are shining and not punctated; blackish to black in color, except the phragmotic part and the legs.

Further description. Holotype: TL 4.1, HW 0.95, HL 0.98, CI 96.9, OD 0.27, SL 0.66, SI 69.5, PW 0.62, PH 0.38, PB 0.24.

Head nearly as wide as long (CI 96.9), sides are nearly straight and not divergent. Eyes are situated behind the midlength of the sides of the head and slightly protruding; their maximum diameter is 0.27 mm or 0.28 HW. Occipital margin and corners in full-face view strongly rounded (Fig. 2 a). Antennal insertion right in the midlength of frontal carinae. Clypeus not convex but strongly angled downwards, forming – together with a small part of the genae and the mandibles – the phragmotic part of the head (Fig. 2 b). Anterior clypeal margin rounded. Mandibles much broader than those of the minors, with lateral borders strongly curved and 5 strong teeth on each masticatory border (Fig. 2 c). Antennal scapes relatively short (SI 69.5); they just reach the occipital margin. Funicular segments become continuously smaller and do not form a distinct club. Frontal carinae extend to less than two-thirds of head length. Apart from a slight projection behind the scapal insertion, they are straight and distinctly divergent. Alitrunk with a deep impression (metanotum) between promesonotum and propodeum, and two raised stigmata beside the deepest point of the impression. Petiolar scale broadly rounded on top.
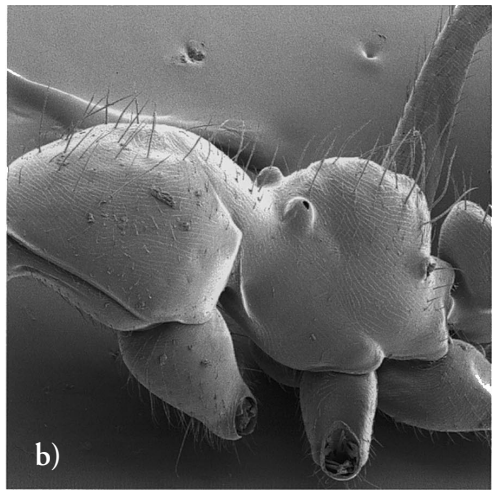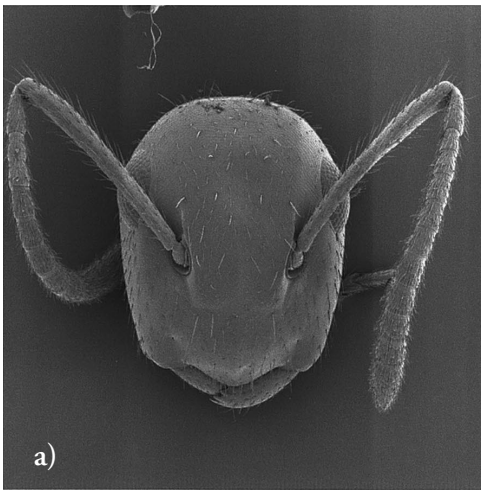

FIG. 3: Scanning electron micrographs of *Camponotus* (*Colobopsis*) *markli* workers, a) head, b) alitrunk.

Nearly whole animal blackish brown to black in color; only legs and front part of head lighter. Surface of all body parts shining. Accordingly, cuticular punctures and reticulated sculptures (SEM) are weak (Fig. 2 a). Decumbent pubescence is lacking on all body parts. Longer erect white hairs on all body parts, especially on antennal scapes and legs.

Paratype (majors) (n = 6): TL 4.1–4.5, HW 0.94–1.06, HL 0.98–1.30, CI 86.1–96.9, OD 0.27–0.3, SL 0.65–0.74, SI 63.7–70.2, PW 0.6–0.68, PH 0.38–0.46, PB 0.23–0.28.

Holotype, eastern Thailand: Khao Chamao, 1. 02. 2001, leg. U. Maschwitz (Naturhistorisches Museum Basel).

Paratype (majors) 4 with the same data as holotype (2 in Museum of Comparative Zoology at Harvard University, 2 in National Museum of Malaysia, Kuala Lumpur) and 2 eastern Thailand: Khao Sa Bap, 3.02.2001, leg. U. Maschwitz (in collection of the author).

Minor workers:

Diagnosis: No intermediate forms between major and minor caste, head trapezoidal and elongated, all body parts are blackish and shining and not punctated. Decumbent pubescence is lacking, longer erect white hairs on all body parts.

Head trapezoidal and elongated (CI 83.7), sides are nearly straight. Eyes are situated behind the midlength of the sides of the head and slightly protruding; their maximum diameter is 0.23 mm or 0.32 HW. Occipital margin and corners in full face view strongly rounded (Fig. 3 a). Clypeus slightly convex and without median carina; anterior clypeal margin rounded. Mandibles relatively short, with lateral borders strongly curved and 4 subequal teeth on each masticatory border. Antennal scapes relatively large (SI 97.2); they project beyond the occipital margin by about one third of their length. Funicular segments become continuously smaller and do not form a distinct club. Frontal carinae extend to about two-thirds of head length. Apart from a slight projection behind the scapal insertion, they are straight and slightly divergent (Fig. 3 a). Alitrunk and petiolar scale as in major worker.

Whole animal dark brown to black in color, only tarsi and mandibles lighter. Surface of all body parts shining. Accordingly, cuticular punctures and reticulated sculptures (SEM) are weak (Figs. 3 a, b). Decumbent pubescence is lacking on all body parts. Longer erect white hairs on all body parts, especially on antennal scapes and legs.

Paratype (minors) (n = 7): TL 3.1–3.4, HW 0.72–0.78, HL 0.86–0.94, CI 85.2–88.3, OD 0.23–0.24, SL 0.68–0.74, SI 92.3–97.3, PW 0.44–0.5, PH 0.34–0.36, PB 0.2–0.22.

Paratype (minors): 7 from eastern Thailand: Khao Chamao, 1. 02. 2001, leg. U. Maschwitz (1 in Naturhistorisches Museum Basel, 2 in Museum of Comparative Zoology at Harvard University, 2 in National Museum of Malaysia, Kuala Lumpur, 3 in collection of the author).

Female sexuals:

Diagnosis: Head elongated, sides are nearly straight. Eyes are situated behind the midlength of the sides of the head; ocelli widely spaced. Mesonotum prominent with steep declivities to pronotum and propodeum. Node of petiole flat on top. Color of head and gaster brown, alitrunk yellowish brown, legs darker.

Head elongated (CI 73.3–74.6), sides are nearly straight. Eyes are situated behind the midlength of the sides of the head and distinctly protruding; their maximum diameter is 0.50–0.52 mm or 0.45–0.48 HW. Ocelli widely spaced (OD1 0.28–0.34 mm, OD2 0.16–0.18 mm). Occipital margin and corners in full-face view strongly rounded (Fig. 4 a). Clypeus not convex but strongly angled downwards, forming – together with a small part of the genae and the mandibles – the phragmotic part of the head (Fig. 4 b). Anterior clypeal margin rounded. Mandibles relatively short, with lateral borders strongly curved and 6 subequal teeth on each masticatory border. Position of antennal insertion right in the midlength of frontal carinae. Antennal scapes relatively short (SI 80.4–97.6); they are long enough to reach the occipital margin. Funicular segments become continuously smaller and do not form a distinct club. Frontal carinae extend to nearly two-thirds of head length. Apart from a slight projection behind the scapal insertion, they are straight and slightly divergent (Fig. 4 a). Alitrunk in dorsal view with the pronotal angles weakly rounded. Seen in profile, mesonotum prominent with steep declivities to pronotum and propodeum, surface of mesonotum only slightly rounded (Fig. 4 c). Petiolar scale in dorsal view broadest behind with rounded corners; seen in profile, node of petiole flat on top, anterior slope steep, posterior slope broadly rounded on top (Fig. 4 d).

Color of head and gaster brown, alitrunk yellowish brown; legs darker. Surface of all body parts shining. Accordingly, cuticular punctures and reticulated sculptures (SEM) are weak (Figs. 4 a, b, c). Decumbent pubescence scarce on all body parts. Longer erect
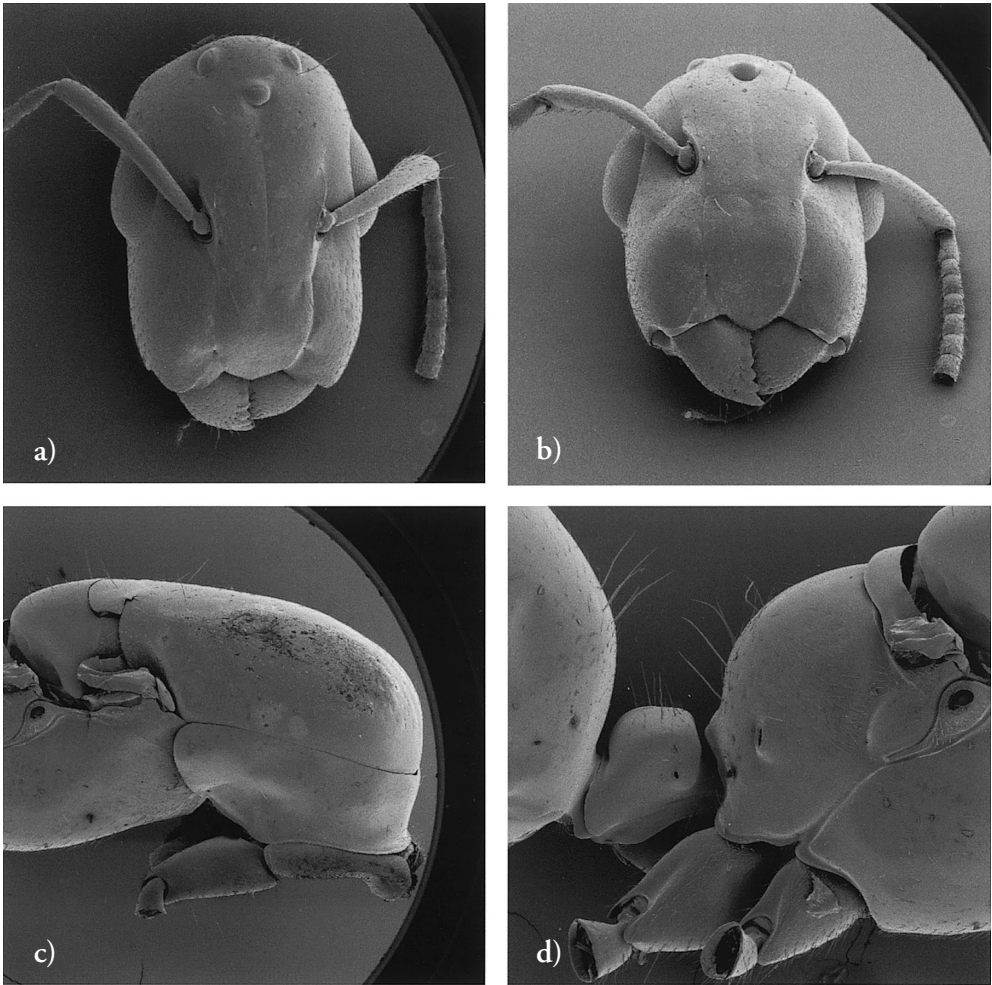
FIG. 4: Scanning electron micrographs of *Camponotus* (*Colobopsis*) *markli* females, a) head, b) phragmotic part of the head, c) alitrunk, d) parts of alitrunk, petiole and gaster.

white hairs on all body parts, especially on antennal scapes and legs.

Paratype (females) (n = 6): TL 7.6–7.9, HW 1.08–1.12, HL 1.46–1.52, CI 73.3–74.6, OD 0.50–0.52, OD1 0.28–0.34, OD2 0.16–0.18, SL 0.86–0.96, SI 80.4–97.6, PW 1.15–1.24, PH 0.44–0.46, PB 0.42–0.48, FWL 7.5–7.8, HWL 5.0–5.1, FWW 2.2–2.2, HWW 1.7–1.7.

Paratype (females): 3 from eastern Thailand: Khao Chamao, 1.02.2001, leg. U. Maschwitz (1 in Naturhistorisches Museum Basel, 1 in Museum of Com-

parative Zoology at Harvard University, 1 in National Museum of Malaysia, Kuala Lumpur), 3 eastern Thailand: Khao Sa Bap, 3.02.2001, leg U. Maschwitz (in collection of the author).

Males:
Diagnosis: Head elongated, sides are nearly straight. Ocelli widely spaced. Color mostly mid brown, altirunk and parts of the legs yellowish brown. Decumbent pubescence especially on gaster but also on the rest of the body parts.
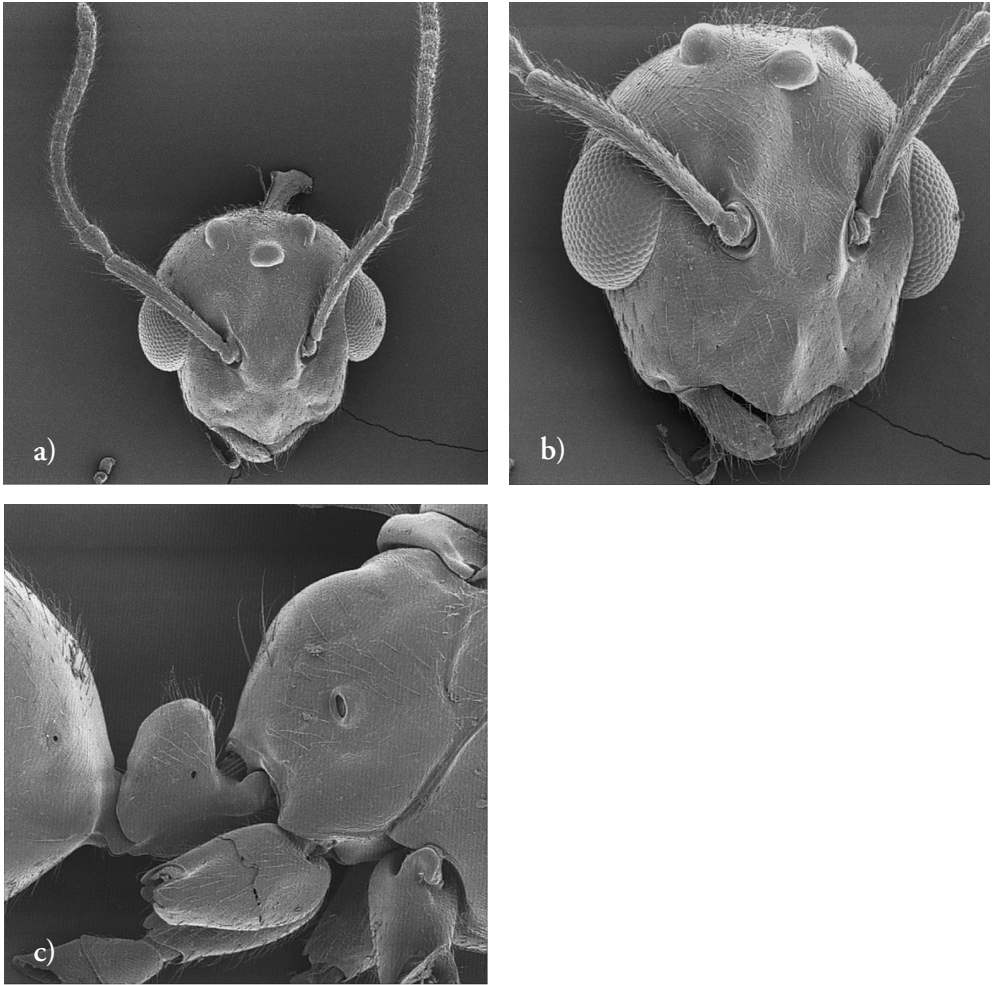
FIG. 5: Scanning electron micrographs of *Camponotus* (*Colobopsis*) *markli* males, a) head with antennae, b) head, c) parts of alitrunk, petiole and gaster.

Head elongated (CI 76.9–89.2), sides are nearly straight (fig.5 a). Eyes are situated midlength of the sides of the head and strongly protruding; their maximum diameter is 0.31–0.33 mm or 0.46–0.55 HW. Ocelli widely spaced (OD1 0.22–0.24 mm, OD2 0.10–0,12 mm). Occipital margin and corners in full-face view strongly rounded (Fig. 5 b). Clypeus strongly convex and with distinct median carina; anterior clypeal margin strongly rounded. Mandibles relatively short, with lateral borders scarcely curved and 3 subequal teeth on each masticatory border which are more or less rounded (Fig. 5 b). Antennal scapes moderately long (SI 72.7 – 83.3); they are just long enough to reach the occipital margin (Fig. 5 a). Funicular segments about equal in width. Frontal carinae extend to about midlength of the head. Apart from a slight projection behind the scapal insertion, they are straight and distinctly divergent (Fig. 5 b). Alitrunk with only a very slight impression between promesonotum and propodeum (Fig. 5 c). Petiolar scale stongly rounded on top.

Color mostly mid brown, altirunk and parts of the legs yellowish brown. Surface of all body parts

shining. Accordingly, cuticular punctures and reticulated sculptures (SEM) are weak (Figs. 5 a, b). Decumbent pubescence especially on gaster but also on the rest of the body parts. Longer erect white hairs on all body parts, especially on antennal scapes and legs.

Paratype (males): TL 3.82–3.83, HW 0.60–0.66, HL 0.74–0.78, CI 76.9–89.2, OD 0.31–0.33, OD1 0.22–0.24, OD2 0.10–0.12, SL 0.48–0.5, SI 72.7–83.3, FWL 4.6–4.7, HWL 2.9–3.0, FWW 1.7–1.7, HWW 1.3–1.3.

Paratype (males), 2 from eastern Thailand: Khao Chamao, 1. 02. 2001, leg. U. Maschwitz (1 Naturhistorisches Museum Basel, 1 collection of the author).

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