Chapter 3

Communication and Sociality

Receptors and senses have been outlined in **chapter 2.2.6**. Their outstanding performance is one of the keys to the success of insects. Receptors are essential devices of a receiver and can be compared with a satellite dish or antenna. A TV set doesn't work without these devices, similarly an insect requires receptors to respond. Communication and behaviour depend on information acquired by receptors.

The simplest type of behaviour might be a **reflex**. This is a simple reaction as a result of a particular stimulus, for instance the spontaneous withdrawal of the hand from a source of heat. There are two types of movements triggered by a simple stimulus. An unoriented action varying with the intensity of the stimulus is called **kinesis**. We talk about **taxis**, if the movement is towards (**positive** taxis) or away from the stimulus (**negative** taxis). According to the quality of the stimulus **chemo-** (related to taste and scent), **geo-** (related to gravity), **hygro-** (related to humidity), **photo-** (related to light), **thermo-** (related to temperature), **phono-** (related to sound) **-taxis** or **-kinesis** can be defined. Using these terms, a positive phototaxis is a movement towards light, for instance a plant growing towards light or a nocturnal insect, like a moth, being attracted to a light source (see also **chapter 7.5**). When an insect follows a gradient, for instance the concentration of a pheromone as shown in **fig. 3-5**, it is called **klinotaxis**. Insect behaviour generally is **innate** and determined genetically, but simple **learning** has been observed in some bees and butterflies.

Different types of **communication** are discussed in this chapter. Communication enables cooperation, without communication no cooperation. One can easily figure out the chaos as a result of a lack of communication and cooperation for example in a termite colony of several million individuals, equivalent to the population of PNG. Complex behaviour based on communication includes **territorial behaviour**, **courtship**, **brood care** and **parental care**. The latter is important for the understanding of how sociality in insects evolved.

This chapter also looks at **insect societies**, following the evolution from simple aggregations to **social insects** culminating in the eusocial termites and Hymenoptera like bees, some wasps and all ants.

3.1 Communication

One might tend to believe that insects do not have much to say, as stated by Piau, J. and Lynch, J. in "Communication and Language - Reader" (UPNG; Waigani; PNG; 1989):

"Insects have a very limited number of messages that they can say or receive. The male of a certain species of grasshopper, for example, has a choice of six messages, which might be translated as follows:

- **I am happy, life is good**
- **I would like to make love**
- **You are trespassing on my territory**
- **She's mine**
- **Let's make love**
- **Oh how nice to have made love**"

Communication between insects is mainly about reproduction, food and territory and definitely not about rugby and politics. Since we are far away from having a holistic conception of the complex communication processes, especially of social insects, we do not exactly know whether or not there are more messages that insects exchange.

Communication is defined as **information** being sent by one individual (**sender**) and perceived by one or several other individuals (**receiver**):

sender → **receiver**
information

The information can be transmitted either between individuals of the same species (**intraspecific**) or between individuals of different species (**interspecific**). The medium for signal transduction in insects is either of **auditory**, **visual**, **tactile** or **chemical** nature.

3.1.1 Auditory Communication

In tropical countries sound-producing insects can be recognised almost all day and night. Amongst those producing sound, cicadas, crickets and grasshoppers are definitely the most conspicuous ones. Cicadas are the animals producing the loudest sounds in terms of sound pressure, although a barking or howling dog might seem louder to us humans. This is because the main frequency range of a cicada is above 20,000 Hz, beyond the detectable frequency range of human beings. **Sonograms** display the frequency of sound waves as a function of time. The sonograms of some insect sounds are shown in **fig. 3-1**.

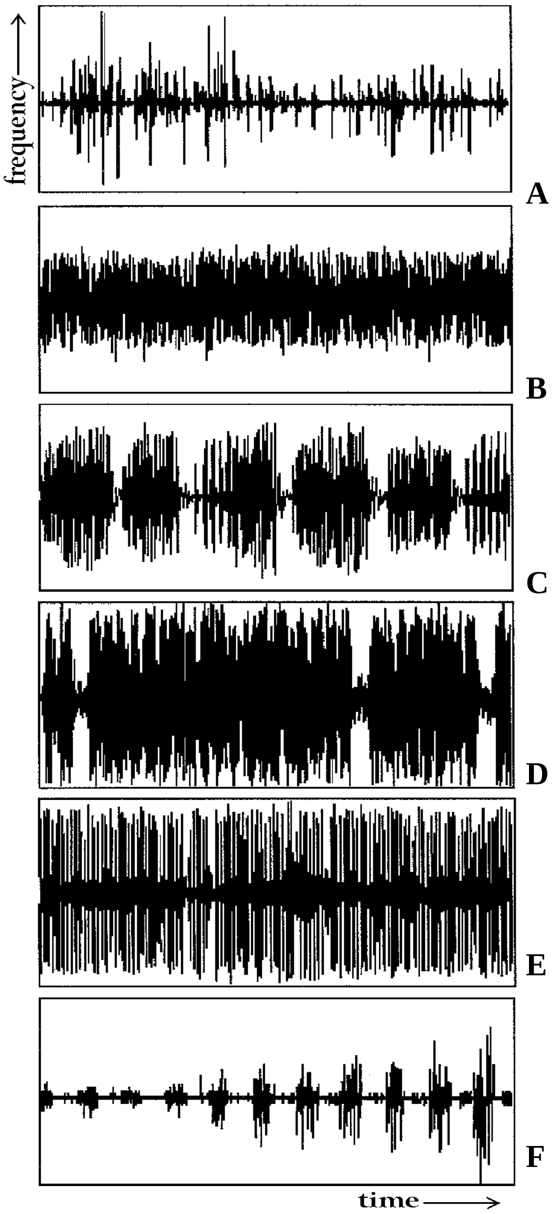

Fig. 3-1: Sonograms of insect sounds: (A) Assassin bug *Canthesancus sp.*, (B) Drummer cicada *Thopa sp.*, (C) Black Field cricket *Teleogryllus sp.*, (D) Bush cricket *Tettigonia sp.*, (E) Mole cricket *Gryllotalpa sp.*, (F) Death's Head moth *Acherontia sp.* (reproduced by permission of CSIRO Australia from CSIRO, 1996[2])

There are several ways of producing sounds:

Air forced through or over small openings causes a **hissing sound**. This can be experienced, when the Rhinoceros beetle *Xylotrupes gideon* is touched.

Stridulation or frictional rubbing is the result of two parts of the body being scraped together. The chirp of a grasshopper or cricket is produced by scraping the front part of the hind wing over the thickened veins of the forewings. Other grasshoppers possess file-like structures on the forewings as shown in **fig. 3-2**, that are rubbed over the inner side of the hind femur. Particular assassin bugs (**Reduviidae**) rub the tip of their proboscis along a file on the ventral part of their abdomen (see **fig. 3-3**).

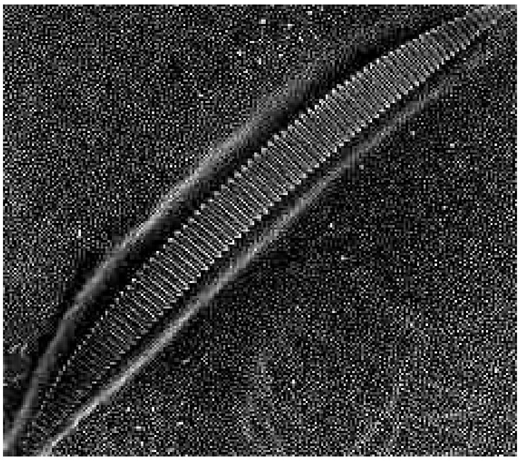

Fig. 3-2: Stridulatory file under tegmen of a Tettigoniidae grasshopper which is rubbed over the hind femur (reproduced from CSIRO, 1991)

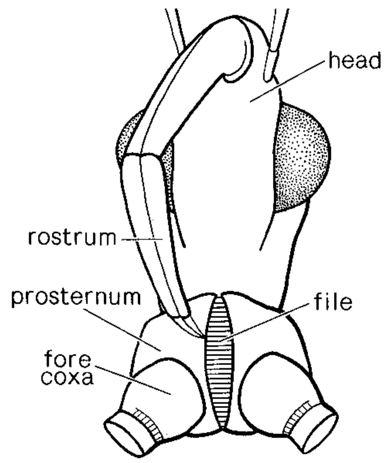

Fig. 3-3: Stridulatory file on ventral part of thorax of a Reduviidae bug. The tip of the proboscis is scraped along the file to produce sound (reproduced from CSIRO, 1991)

A **vibrating membrane** called a **musical apparatus** is used by cicadas for the production of sound. One out of a set of several membranes in ventral pouches at the base of the abdomen (see **fig. 3-4**) is connected with a muscle, that pulls the membrane inwards. Upon relaxation of the muscle, the membrane snaps back, causing vibrations that are amplified by other membranes. This process is repeated several thousand times per second.

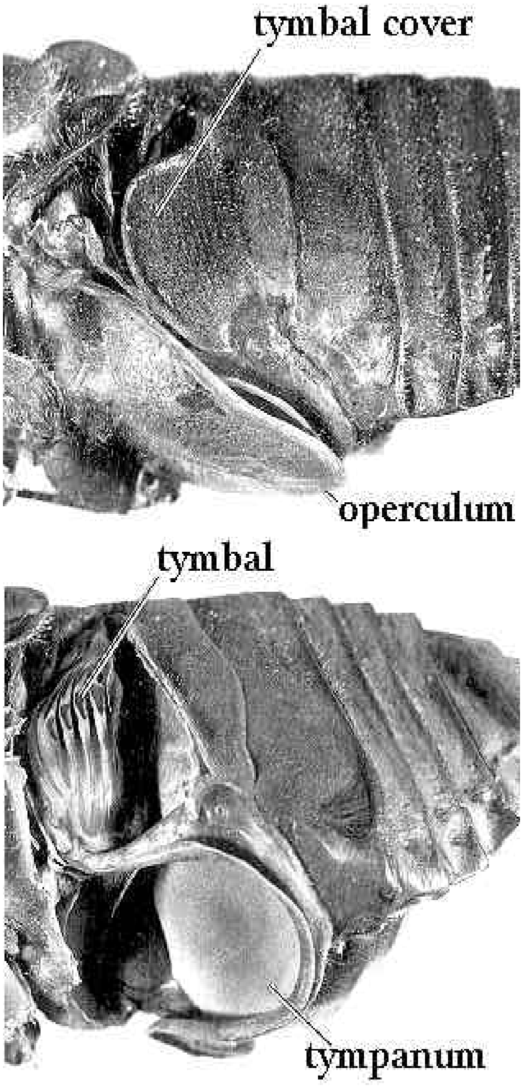

Fig. 3-4: Musical apparatus of a cicada (Cicadidae). Tymbal cover and operculum removed at bottom (reproduced from CSIRO, 1991)

Beating substrate with parts of the insect body is done for instance by some termite soldiers hitting wood with the tips of their mandibles or by some grasshoppers using their hind tibiae as drum sticks, hitting the ground.

The production of sounds serves various purposes. Some insects mark their territory by means of sound and for many, sound is the medium of communication for courtship and reproduction. The hissing sound of a Rhinoceros beetle upon disturbance is definitely a defence strategy. Other examples for audible defence are particular Tiger moths (**Arctiidae**). These animals are able to produce and detect ultra sound. Bats use ultrasound for their echolocation system in order to detect obstacles and prey during the night. Tiger moths thus are able to recognise an approaching bat. A number of disastrous Tiger moths use ultrasound to tell the bat: “I am distasteful, unpalatable to you, leave me in peace”. Other Tiger moths make a lot of ultrasonic noise and in this way disturb the bat’s echolocation system. As a result of this interference, the bat loses orientation and cannot get the moths.

3.1.2 Visual Communication

Visual communication seems to be well developed in insects for various purposes. Bright coloration (warning or **aposematic** coloration) of wings and other body parts, as is the case in many moths and butterflies (**Lepidoptera**) and in bees and wasps (**Hymenoptera**), plays an important role for defence as visual **mimicry** (see **chapter 4.4.5**). Colours also stimulate sexual behaviour. Some insects have the ability to display glowing light in darkness, a phenomenon, called **bioluminescence**. This is an energy requiring reaction triggered by the enzyme **luciferase**. Common examples are beetles like fireflies and their larvae, the glow-worms (**Lampyridae**), click beetles (**Elateridae**), some springtails (**Collembola**), the lantern bug (**Fulgoroidae**) and a few species of true flies (**Diptera**). Bioluminescence is used for courtship signalling and prey-luring.

3.1.3 Chemical Communication

The most important means of communication in insects is the use of chemical signals involving the senses of smell and taste. No other group of animals has developed such a variety of hundreds of chemical substances for the communication between all stages of the life cycle and sexes. These communication chemicals or **semiochemicals** are produced by **exocrine glands** and released into the environment. Generally they can be classified as **pheromones** and **allelochemicals**.

The volatile **pheromones** are used for communication within individuals of the same species as **trace indicators** for instance by ants, as **courtship pheromones** and **sex attractants** eg. by moths, as **aggregation pheromones**, **spacing pheromones**, **alarm indicators** and for the **control of castes** in social insects. The location of a female, emitting a sex attractant is shown in **fig. 3-5**. Sex attractants can be used for the biological control of certain insect pests. A trap can be baited with the pheromone in order to lure and kill the males, but more commonly an artificial sources of pheromone is placed in the pest-infested area. The artificial pheromone superimposes the pheromone trails of females, thus confusing the males and making it impossible for them to locate the females. Like most of the semiochemicals, pheromones act specifically on one particular species. That is the reason why there is only a very limited number of quite expensive pheromones available for biocontrol purposes.

Allelochemicals facilitate communication between individuals of different species. These substances can be further grouped into **kairomones**, **allomones** and **synomones**. Kairomones benefit the receiver but disadvantage the producer. An example is the host-plant detection by a phytophagous insect. Termites or bark beetles are attracted to the scent released by a damaged, thus weakened host-tree. Allomones benefit the producer, but have no effect on the receiver as is the case with defensive chemicals. Synomones are advantageous for the producer and the receiver. Using the damaged host-tree of the above example, a parasitoid of the bark beetle benefits from the allelochemical. The parasitoid is attracted to the damaged tree and finds its host, the bark beetles. As the bark beetle gets killed by the parasitoid, the tree benefits as well because there are fewer bark beetles, attacking it.

3.1.4 Tactile Communication

Tactile communication uses touch as its medium. Ants for instance drum the abdomen of particular plant lice (**Aphididae**) with their antennae. This signal makes an aphid release a sweet excretion from its anus, that is readily taken by the ant.

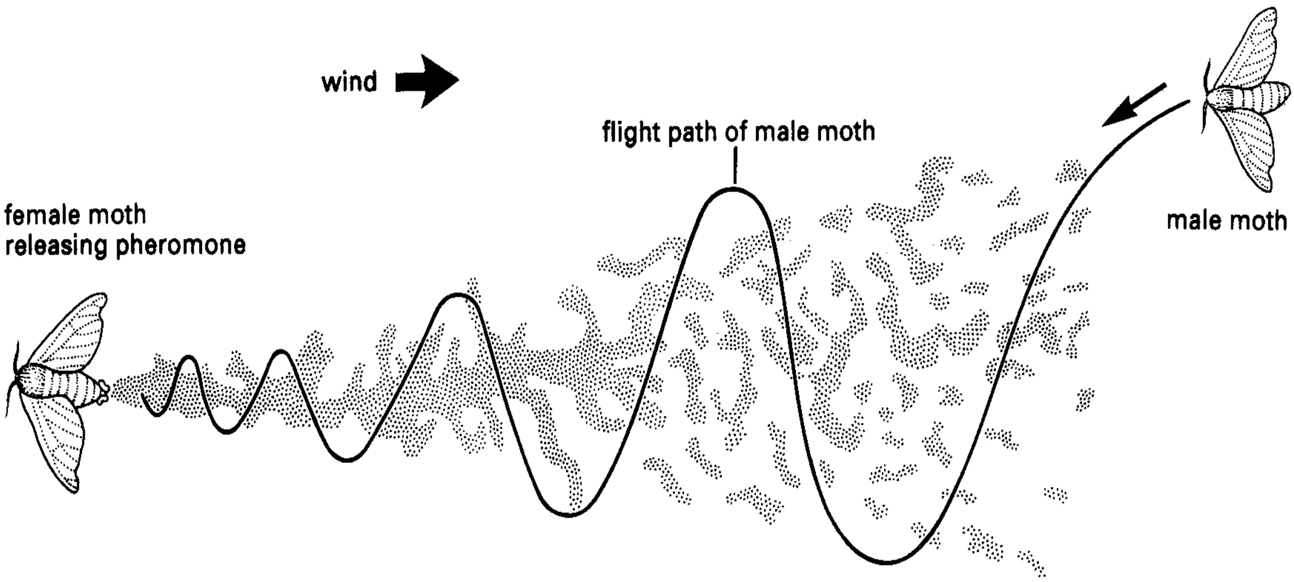

Fig. 3-5: Male moth locating a female releasing a sex attractant. The male follows a gradient of increasing concentration of the pheromone (reproduced from Gullan, P.J. and Cranston, P.S., 1994)

3.2 Insect Societies

The degree of social organisation of insects shows an almost gradual increase in complexity from **solitary** or singly living individuals of particular species, through subsocial **aggregations** of individuals of a species to **presocial** (**communal**, **quasisocial** and **semisocial**) species, culminating in highly organised **eusocial** species, the truly social insects.

Subsociality

The vast majority of insects are solitary, living singly without exhibiting social behaviour. The next step towards sociality are non-reproductive **aggregations** of insects. Forming aggregations increases the chances of survival. Commonly encountered are roosting aggregations as shown in **fig. 3-6**. During the beginning of 1998, hundreds of this particular noctuid moth could be observed gathering around security lights and making a nuisance of themselves.

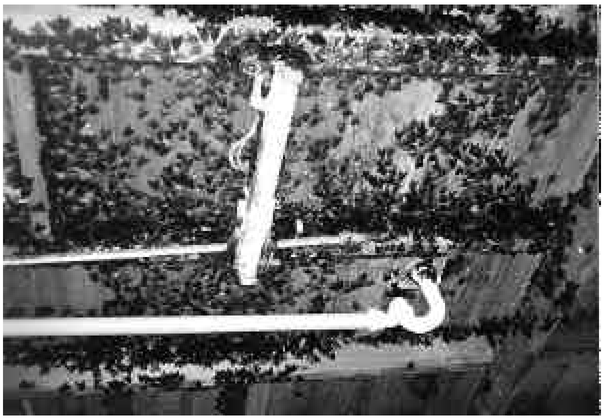

Fig. 3-6: Roosting aggregation of the Noctuidae moth *Nagia episcopalis* (photo Schneider, M.F.)

Another interesting example is the migrating locust or plague locust. These animals are usually **solitary**. Periodically, when climatic and other conditions are suitable, the locust population booms. The insects then aggregate during the course of several generations and successively become **gregarious**. The nymphs can form 'hopper bands' of the size of several hectares, with densities illustrated in **fig. 3-7**. Adults aggregate into huge swarms that can fly long distances without break. Nothing can stop grasshoppers from eating almost anything that is green. Thus, plague locusts can cause considerable damage to pasture and food crops. The change in behaviour from solitary to gregarious is closely associated with morphological and physiological changes, a phenomenon called **phase polymorphism**. The changes can be so drastic that scientists considered the two phases as different species. Some morphological differences between solitary and gregarious *Locusta migratoria* are shown in **fig. 3-8**. The slightly smaller gregarious insects have a saddle-like depression on the pronotum and smaller hind femora in relation to the body and wings. Intermediate morphologies occur in transient stages, the stages during the transformation from solitary to gregarious and vice versa. Phase polymorphism is mainly determined by

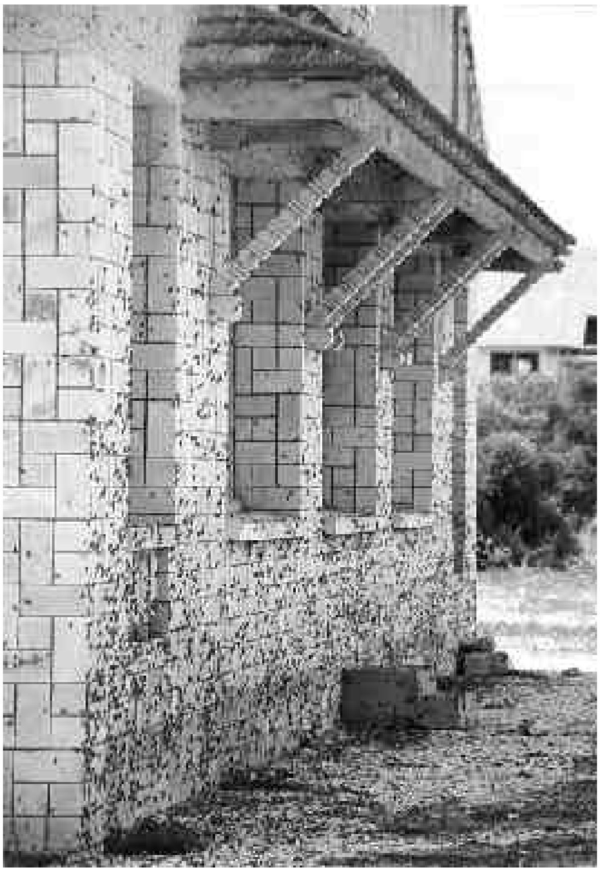

Fig. 3-7: Aggregation of the African locust *Locusta migratoria*, gregarious phase in south-western Madagascar during a plague in 1993. The grasshoppers enjoy the warmth radiated by the bricks (photo Holtmann, M.)

the population density and to a certain extent by the presence of a pheromone. High densities of locusts have a positive feed-back on the gregarious phase via tactile stimuli. *Locusta migratoria*, mainly a pest in Africa, can also be found in the Markham Valley, causing severe damage to pasture and crops like corn and rice. Other species of plague locusts are the Desert locust *Schistocerca gregaria*, occurring between northern Africa and Pakistan and *Nomadacris guttulosa* in Australia and New Guinea.

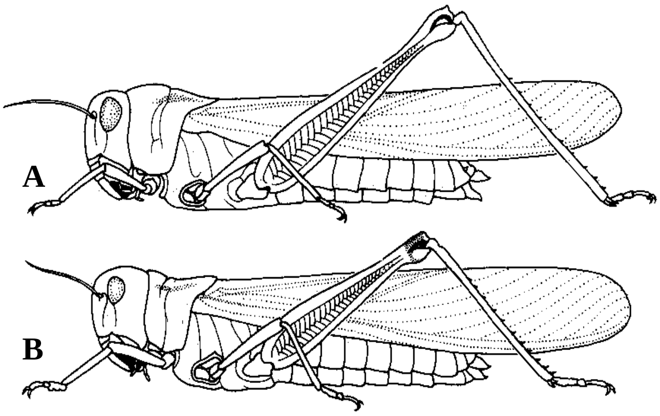

Fig. 3-8: Morphological differences between solitary (A) and gregarious (B) phases of *Locusta migratoria*. See text for more details (reproduced from Gullan, P.J. and Cranston, P.S., 1994)

Social Insects

The highest behavioural complexity can be found in truly social (**eusocial**) insects, that show the outstanding feature of **social organisation**. Of course, **cooperation** and **communication** are basic prerequisites for social behaviour. Social organisation in this context means that the individuals live together as a **colony**, sharing the same nest. Social animals are restricted to the insect class with one single exception, the **naked mole rat** *Heterocephalus glaber* of the mammal order **Rodentia** (**Bathyergidae**). Social insects belong to only two insect orders and include all species of termites (**Isoptera**) and certain species of **Hymenoptera**, ie. all ant species and some bee and wasp species. **Eusocial behaviour** is defined as:

- cooperation of individuals in the care of the young (**parental care**)
- specialisation of distinct groups in a colony (**caste system**)
- overlap of at least two generations in the life cycle of the individuals

According to this definition, plague locusts and humans for instance are not eusocial animals.

Eusocial insects exhibit structurally and functionally specialised groups of individuals. This specialisation is referred to as **caste system** of **reproductives**, **workers** and/or **soldiers** with each caste having its specific tasks to fulfil. Which caste a particular individual will belong to is controlled by one or more of the following factors: pheromones, the type of food, the age of an individual, haplodiploidy and other mechanisms not yet well elucidated. The **colony size** might vary from 30,000 to 50,000 individuals in bees to up to one or even 22 million individuals in termite and ant colonies.

3.2.1 Termites

The fascinating but complex biology of termites is in many regards still a mystery to the numerous scientists dedicated to termite research. As decomposers remineralising dead plant material, the animals play an outstanding role in the food chain. However, a large number of termite species are of economic importance as pests in agriculture, forestry, architecture and building. Effective control measures against termites are not really available due to a fragmentary understanding of termite biology.

The simplified model of a termite life cycle, shown in **fig. 3-9**, indicates the three castes, the **reproductives**, the **soldiers** and the **workers**. Due to the fact that termites are hemimetabolous insects, even the nymphs take part in the social life and have their specific tasks to fulfil. The so far poorly understood concept of caste determination does not seem to be definitive or too rigid. Once the caste of an individual is determined, development into other castes is still possible. Soldiers, also referred to as **intercastes** might turn into workers or even into reproductives, if there is a shortage of individuals of other castes. This process is controlled by **pheromones**. In the case of the queen, there is a specific 'queen' pheromone, preventing other individuals from turning into queens. Only if the queen is removed or dies, does the lack of the specific pheromone promote the development of a new queen. The morphological differences of individuals of different castes are shown in **fig. 3-10**.

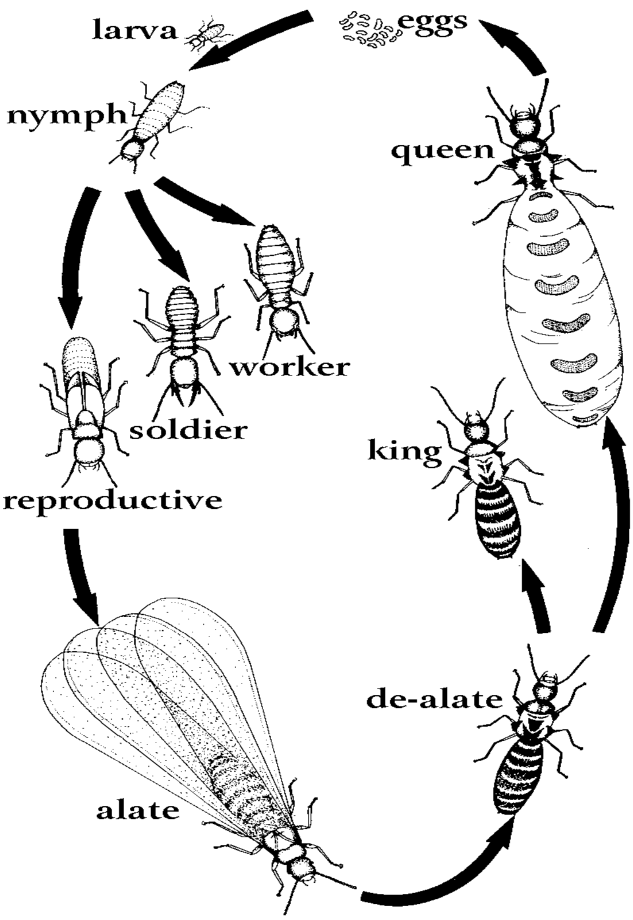

Fig. 3-9: Termite life cycle (reproduced with permission from Hadlington, P., 1992)

Reproductives possess compound eyes and are more or less brown due to their sclerotized cuticle. Developing reproductives have wing buds, wings or wing stumps. Reproductives can be further divided into:

- **Alates**, the young winged reproductives of both sexes. From time to time about 100 to 1000 alates leave the colony for a mating and colonising flight. After mating a pair settles down at a suitable site like a rotting scar on a tree in order to establish a new colony.
- **De-alates**, alates that cast their wings after the colonising flight and successively turn into queens and kings. Initially only a few eggs are laid and brought up by a female de-alate. As the number of individuals in the colony grows, the more workers are available to help the young queen to care for the brood. After three to five years the number of individuals is already so large, that the colony of a pest species can turn into the damaging stage.
- **Queen** and **king**, which are the main reproductive individuals in a colony. Once there are many workers to help the queen, her only job is to produce a tremendous number of offspring. A large queen may lay more than 1000 eggs per day. The life span of a queen can be as much as 50 years.
- **Neotenics** assist the queen in laying eggs, once her productivity decreases. When the queen has died or deteriorated, one of the neotenics takes her place. That is the reason why the removal of a queen from her colony does not necessarily mean the end of the colony.

Workers are sterile, wingless and blind males and females. Their cuticle is unpigmented and not hardened, therefore the animals are confined to a dark and moist environment. Workers build the nest and galleries, they fetch food, care for the brood and feed reproductives and soldiers. The worker's life span is one to two years.

Soldiers are, like workers sterile, wingless and blind males and females with an unpigmented, unsclerotized cuticle. Soldiers defend their colony from intruders by the use of powerful jaws and/or by ejecting a white sticky repellent from an opening on their head. Soldiers can't feed themselves, they have to be fed by workers. Usually the number of soldiers is much smaller than the number of workers. Soldiers can be **mandibulate** or **nasute**, shown in **fig. 5-17**, depending on the species. Therefore soldiers can be used

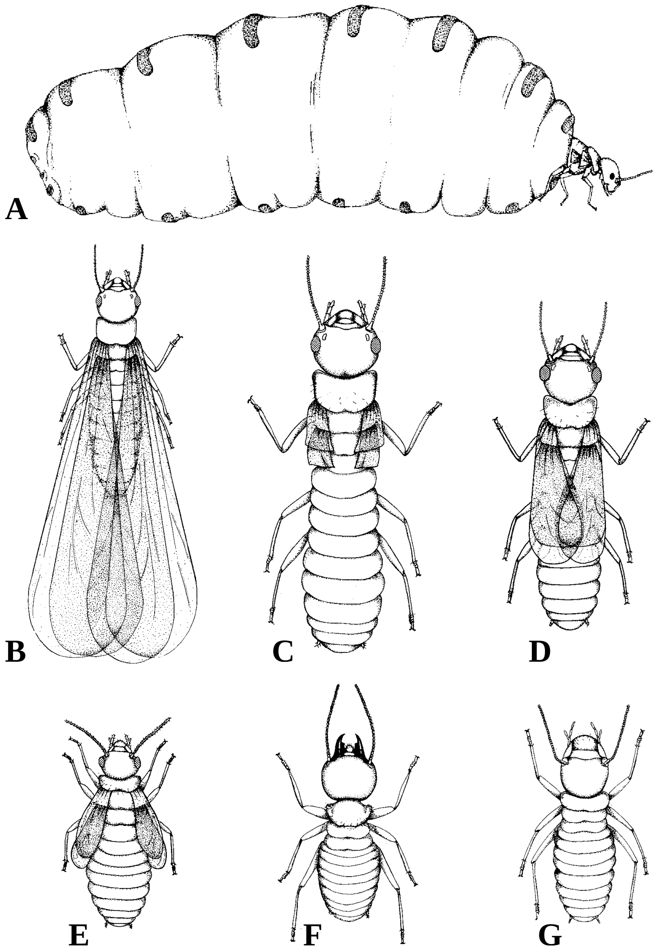

Fig. 3-10: Castes and different stages of the development of termites (A) mature queen, (B) winged reproductive (alate), (C) de-alate, (D, E) developing reproductives, (F) mandibulate soldier, (G) worker (reproduced with permission from Hadlington, P., 1992)

for the identification of termite species. The life span of the soldiers is one to two years.

As **decomposers** termites feed on living or decaying wood. A major compound of wood is **cellulose**, a carbohydrate like starch. Breaking down cellulose requires an enzyme called **cellulase**. Some termite species have the ability to produce this enzyme, others live in **mutualistic symbiosis** with certain intestinal bacteria or protozoa, that provide the required cellulase. In order to cover their protein requirements, termites feed on fungi, growing on decaying wood. The importance of fungi for termites can be seen from the fact that a young queen on her colonising flight carries a bit of the fungi cake in her mouth. Once she settles down to found a new colony, she inoculates chewed wood with the fungus.

Most termite species are harmless to timber and timber products, but others are even so hungry that they chew the plastic insulation of subterranean power and telephone cables.

Termitarium (Nest)

The queen, the brood and most of the colony's individuals live in a so-called **termitarium** (plural: **termitaria**). It is composed of mud that is sometimes as hard as concrete and a paper-like substance made from chewed wood, as shown in **fig. 3-11**. The conditions inside the nest are dark, moist and cool and suit the requirements of the mostly blind unpigmented termites with their soft cuticles. Runways or **galleries** are built by the workers radially from the nest in all directions and connect the termitarium with

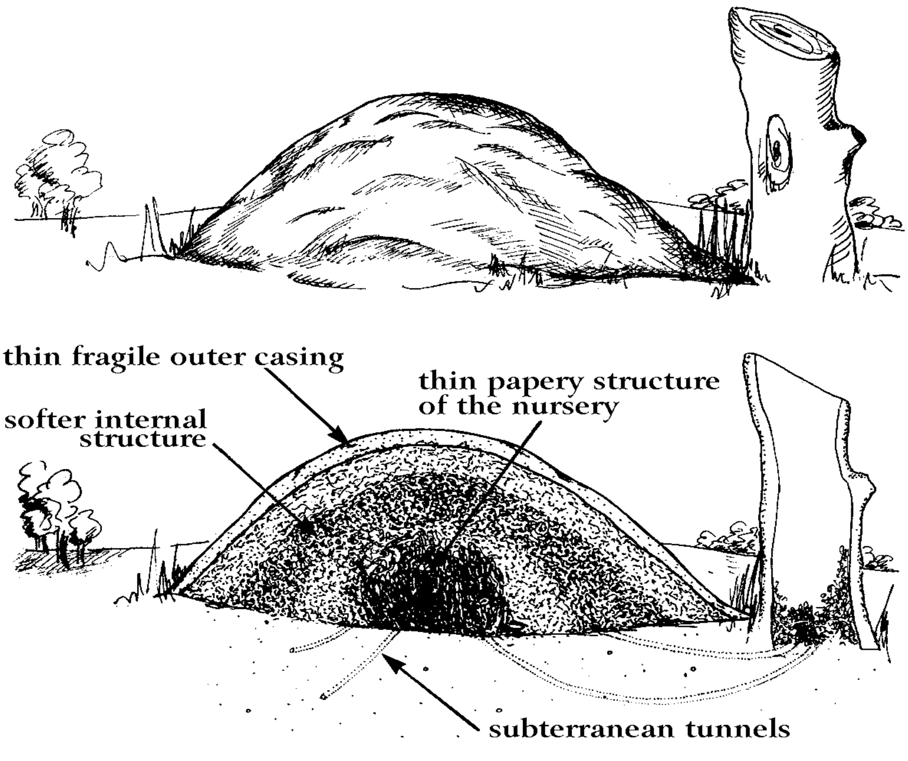

Fig. 3-11: Mound nest of *Nasutitermes spp.* showing the internal structure (reproduced with permission from Hadlington, P., 1992)

Fig. 3-12: Mound nest of *Amitermes meridionalis*; north/south view of the mound (reproduced with permission from Hadlington, P., 1992)

sites where the colony gathers food. These galleries are either **subterranean** about 20 to 50 cm deep or are built from mud (**mud packs** or **mud galleries**), attached to a stem or other substrates. The termites' road system can be enormous and reach a radius of 50 to 100 metres around the nest.

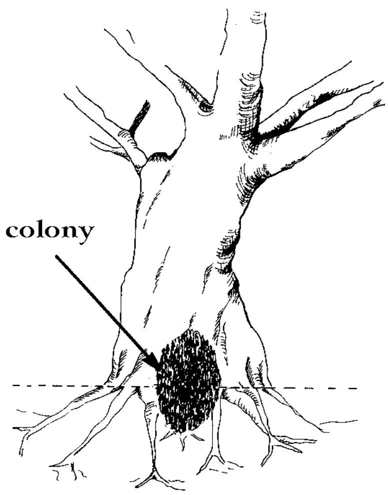

Fig. 3-13: Subterranean nest of *Coptotermes spp.* (reproduced from Hadlington, P., 1992)

Each termite species builds its particular type of nest, either a **mound nest** (**figs. 3-11** and **3-12**) made above the ground, or a **subterranean nest** (**fig. 3-13**) in a buried log, a decaying stump or the crown root of a tree, or an **arboreal nest** attached to a branch or to the stem of a tree (**fig. 3-14**). Mound nests can reach a height of up to six metres. The mound nest of the Australian species *Amitermes meridionalis* is flattened and the tapered sides always orientate towards the north and south as shown in **fig. 3-12**. Constructing the nest this way ensures that the inside of the nest is not heated up by the sun since only the narrow sides are exposed to direct sun light. Subterranean nests buried at a depth of 50 cm or even reaching depths of several metres, are invisible and therefore difficult to discover.

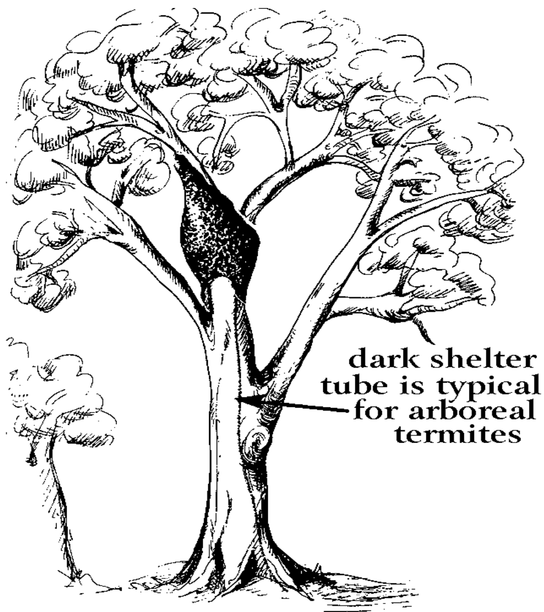

Fig. 3-14: Arboreal nest of *Nasutitermes spp.* (reproduced with permission from Hadlington, P., 1992)

3.2.2 Bees

Bees are the only insect tolerated in a close relationship with man. Bees are always the good characters in fairy tales and other stories and a symbol for endeavour and industrial work. As an utterly beneficial insect, bees were domesticated by man since ages for the production of honey and wax. Thus bees were intensively studied so that much of their complex behaviour is well elucidated. The

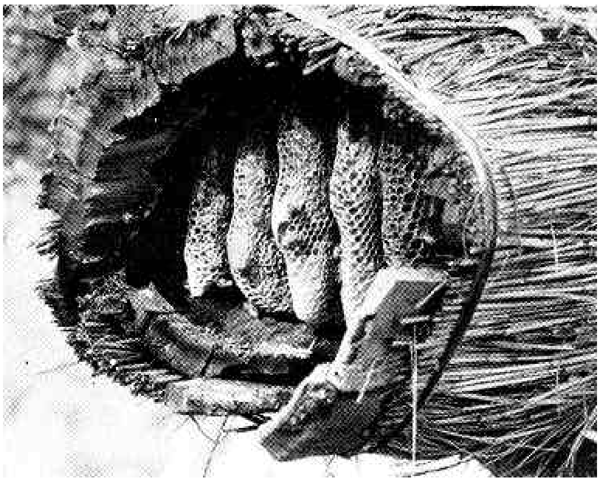

Fig. 3-15: Opened man-made bee hive of the honey bee *Apis mellifera* showing an array of honey combs (reproduced from Clauss, B. & R., 1991)

importance of bees for some cultures is expressed by the fact that in some European countries a three year apprenticeship is required to become a certified tradesman in bee keeping.

Bees live in nests, that are usually built from a paper-like material originating from chewed wood. The nests are either housed in a protected opening such as a hollow tree, or suspended from a branch. The **honey combs** inside the nest are made from **wax** and are used for the storage of honey and to house the brood. Man provides artificial **bee hives** as shown in **fig. 3-15** for domesticated **honey bee** species like as *Apis mellifera*. To collect honey, the combs are removed from time to time and centrifuged. This procedure requires a skilled and calm bee keeper to avoid disturbance of the bees and the resulting painful stings. Apart from honey and wax, the nutritious **royal jelly** has been utilised by man for centuries in traditional medicine. It is a special diet for developing queens, made from nectar and pollen.

PNG has quite a potential for producing honey but despite various organisations running extension programmes, honey is produced in only a few areas like Menyamya and Wau in Morobe Province and in the Eastern Highlands Province.

A colony of the honey bee consists of 30,000 to 50,000 individuals. Two distinct castes can be found, the **reproductive** queens and drones and the **workers**. The **queen's** only task is to lay eggs. Her life span is four to five years. The haploid males, called **drones**, leave the nest where they were brought up and search for young queens to mate with. Once mating is over, the drones are thrown out of the nest and eventually die, since they are unable to care for themselves. Therefore a drone is sometimes called '**flying penis**'. The life span of an adult drone is only a few days. The exclusively female **workers** undergo a change of specialisation during their life. During the first ten days after final emergence their task is to care for the brood, ie. to feed the larvae with honey and pollen. During the next stage of their life they produce honey from nectar, brought in by the collector bees. They also build honey combs from wax, that is excreted by ventral glands on the abdomen. Later in their lives, they dispose of rubbish from the nest, undertake their first flights in the vicinity of the nest and control incoming bees. The last task workers have to fulfil in their life of several weeks is to collect nectar and pollen from the close neighbourhood of the hive or from flowers up to several kilometres away.

All female individuals are **diploid**, the result of sexual reproduction. The males are **haploid**, derived from parthenogenesis. This kind of reproduction and sex determination is called **haplodiploidy** and is further outlined in **chapter 2.2.8**. Unlike termites and other social insects, the castes of bees are determined by the type of diet the developing larvae feed upon. Larvae supposed to become queens are fed with **royal jelly** and are kept in specialised cells of the honey comb. Those larvae bound to become workers are fed with honey and pollen only.

In a bee colony, consisting almost purely of diploid females, the driving force to develop social behaviour is the fact that all workers are sisters, being more closely related to each other than to a daughter or a haploid brother.

An example of the outstanding abilities of insects to communicate is the **waggle dance** of bees. A foraging bee having found a rich source of nectar or pollen performs this dance in the hive upon arrival in order to let the other bees know where to successfully search for food. **Fig. 3-16 A** shows the round dance, that is performed, when the food is close to the hive. The waggle dance (**fig. 3-16 B**) is performed when the food source is distant and gives the direction for getting there. The intensity of both dances indicates the amount of the food in the source: the richer the source the more often the bee repeats the dance. The waggle dance is performed on the vertical part of a honey comb. The angle between the perpendicular line and the straight waggle line of the bee describes the angle between the sun and the food source. As shown in **fig. 3-17 A**, the bee dances straight downwards, meaning that the food source is in the opposite direction to the sun. In **fig. 3-17 B** the angle between the perpendicular line and the bee's straight waggle line is 70°, indicating that the food source can be found 70° left of the sun.

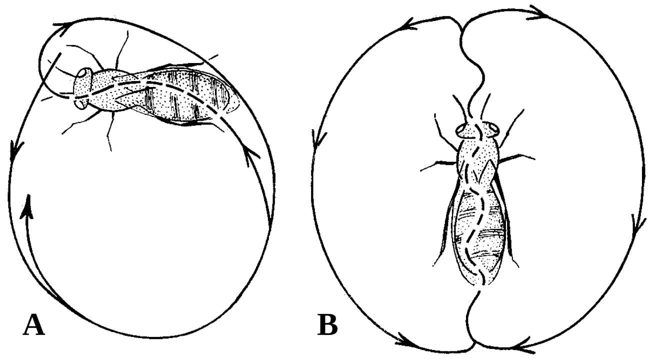

Fig. 3-16: The dance of the honey bee. (A) round dance, (B) waggle dance. See text for explanation (reproduced from Ross, H.H., 1982)

In **fig. 3-17 C** the bee dances vertically upwards indicating that the food source is in the direction of the sun.
Even if the sun is covered by clouds, the bees can still recognise the direction of the sun due to their ability to see **polarised light**.

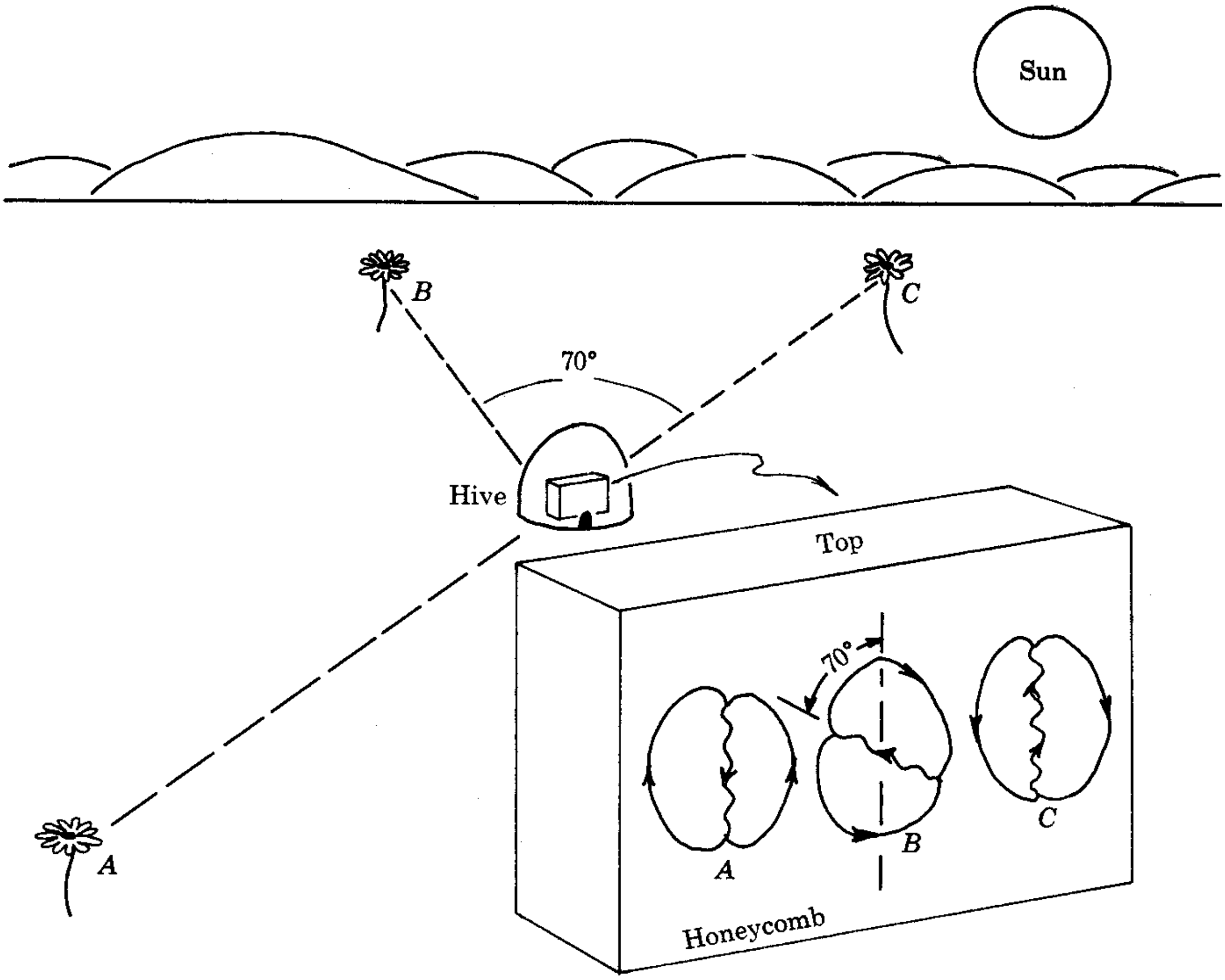

Fig. 3-17: The waggle dance of the honey bee *Apis mellifera* indicates the direction of the food source. See text for explanation (reproduced from Ross, H.H., 1982)

3.2.3 Ants

All ant species are organised in colonies and their caste system is similar to bees. There are amazing and even incredible facts about the life of ants described by Hölldobler, B. and Wilson E.O. (Journey to the Ants - A Story of Scientific Exploration, 1994) and by Hoydt, E. (The Earth Dwellers - Adventures in the Land of Ants 1996). Referring to ants' altruistic dedication to cooperation, the famous **myrmecologists** Hölldobler and Wilson state in 'Journey to the Ants':

"It would appear that socialism really works under certain circumstances. Karl Marx just had the wrong species"

According to the motto 'all for one and one for all', cooperation enables ants to achieve aims that would be impossible for a single ant. Cooperation amongst ants can be easily observed in and on a nest of the arboreal red ant *Oecophylla smaragdina* or **kurakum**. As soon as a nest is damaged, for instance by an object poked into the nest, an armada of ants appears to defend their home. At the same time the ants start to fix the nest by weaving leaves together with a silken thread. Many hands (or legs) cooperate to pull a leaf closer towards the nest, so that it can be tied and attached to the nest, as shown in **fig. 3-18 A**. If a desired leaf is more than one ant-length away from the nest, the insects form long chains of several or more ants, to get the leaf into the right position (see **fig. 3-18 B**). And if twenty or thirty ants are not powerful enough to get the job done, then another hundred ants rush to assist. Large numbers of ants form 'wire-bridge'-like structures as can be seen in **fig. 3-18 C**. These 'bridges' are not only used for towing on the ants' construction sites, but are also formed to cross creeks or to conveniently travel across gaps like from one tree to another. The worker ants do not have the ability to spin a thread. This is done by their larvae, which are carried from the nest's inside to where the silken thread is required.

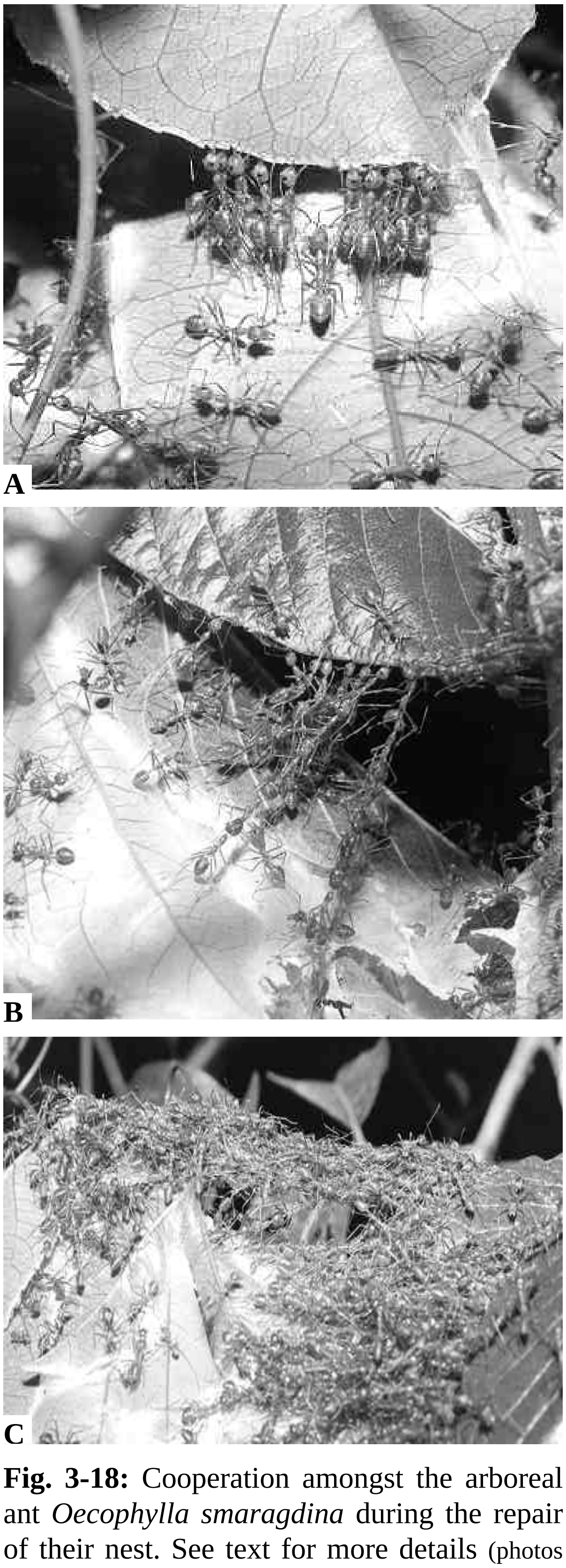

Fig. 3-18: Cooperation amongst the arboreal ant *Oecophylla smaragdina* during the repair of their nest. See text for more details (photos Schneider, M.F.)

Some ant species have developed strange and bizarre forms of **parasitism** and **mutualism** as adaptations to nutrition. These include fungus farming, tending of plant lice and scale insects, slavery and stealing of food, social stomach and mutualism with antplants.

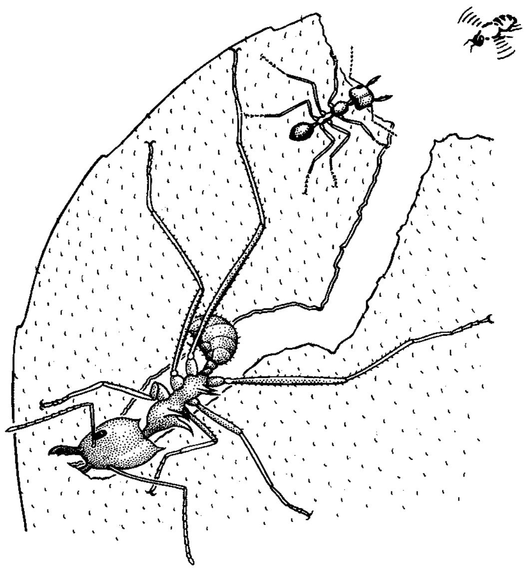

Fig. 3-19: Leaf-cutter ants supply their fungus gardens with pieces of leaves. The medium-sized worker cuts a leaf while the minor worker guards from parasitic flies that lay their eggs on the ants (reproduced from Gullan, P.J. and Cranston, P.S., 1994)

Farming
Some ant species grow fungi in gardens, that are either fertilised with the ants' own faeces or with collected plant material. The latter is done by leaf-cutter ants as shown in **fig. 3-19**. The fungi are harvested by ants as a source of food. The importance of the fungi for the ants is illustrated by the following example: as with termites, a young winged queen takes a piece of the fungi cake into her mouth before she leaves to found a new colony. Once settled down she inoculates plant material with the stored fungus.

Animal Tending
Many ants live in close association with plant lice (**Aphididae**) or scale insects (**Coccidae**). By drumming on the tip of the aphid's abdomen, the ant is stimulating the release of sweet 'faeces', called **honeydew**. Honeydew is readily consumed by the ants. Since **shepherd ants** like this sweet *pekpek* very much, they watch their colony of aphids, so that no other ants come to 'milk' their herd. Other species went one step further, and built bowers for the aphids to live in. During winter in temperate areas, the aphids are brought into the ants' nest and taken back to their host plant the next spring. The highest level is shown by some ant species that rear aphids or scale insects in their nest. The plant lice are brought to their food plants in the morning and taken back to the nest in the evening. In case of disturbance, aphids or scale insects are defended by the ants. The queen takes a fertilised aphid with her to found a new colony. **Fig. 3-20** shows scale insects living together with their guarding ants in a hollow internode of an antplant (**myrmecophyte**).

Guest Ants
Some ant species with very small workers build galleries into nests of larger ants to steal their food. But not all species steal their food, some beg for it. Others live as parasites in termite nests. They avoid being attacked by the termites by imitating the termites specific scent. This kind of defence strategy is known as **mimicry** and uses **allelochemicals** (see **chapters 3.1.3** and **4.4.5**).

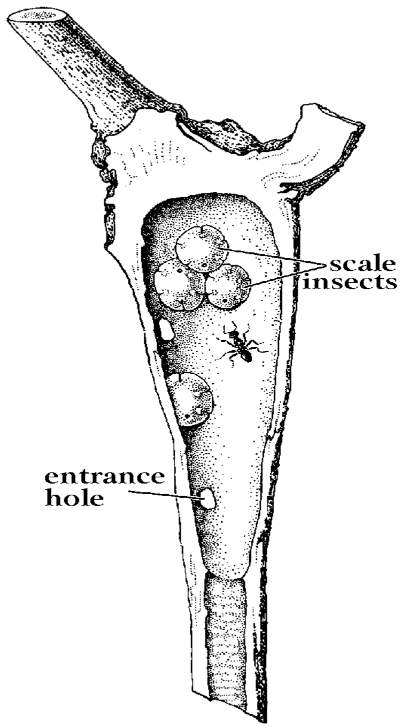

Fig. 3-20: Scale insects excrete honeydew as food for ants. In return, ants provide shelter and care for their scale insects. In this case the scale *Myzolecanium sp.* (Coccidae) and the ant *Anonychomyrma sp.* live together in a hollow internode of the antplant *Kibara sp.* (Monimiacaea) (reproduced from Gullan, P.J. and Cranston, P.S., 1994)

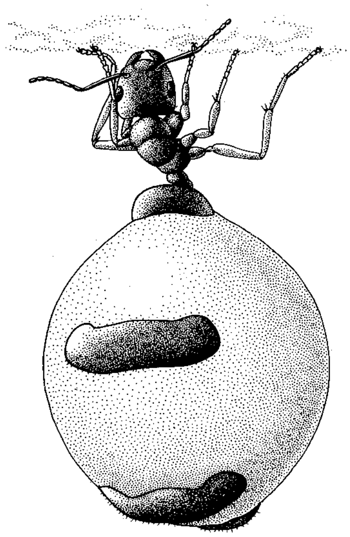

Fig. 3-21: A specialised worker of the honeypot ant *Camponotus inflatus* serving as a live honey storage container for the colony (reproduced from Gullan, P.J. and Cranston, P.S., 1994)

Slavery

Particular ants steal pupae of other ant species and take them to their nest. After the final emergence of the slave ant, it has to do all the work like nursing the brood and cleaning the nest. Other species intrude into nests of foreign ants and bring along their own brood, that is then cared for by the foreign slaves. Queens of some species intrude into a nest, steal several pupae and keep them close to them. After the abducted pupae have hatched, the slave ants have to tend the queen. Other queens move into the nests of the same species, kill the queen and take her place. Queens of particular other species intrude into nests of other species and decapitate (behead) the queen, a process, that takes several hours. The eggs laid by the intruding queen are tended by the slaves. The most alienating example might be the particular species of a slave-keeping ant, that produces only reproductive offspring. Workers of this particular species are not required any more, since workers of other species are used to ride on and to provide food.

Honeypot Ants as Social Stomach

Specialised workers of honeypot ants serve as live honey storage containers. Honey is collected by normal worker ants and fed to the 'honeypot' ant. This animal holds the honey in the considerably expandable abdomen, as shown in **fig. 3-21**. The ability to enlarge the abdomen to this extent is due to the stretchable **arthrodial** or intersegmental membrane. The honey is later released for the consumption by other ants of the colony. The temporary holding pouch inside the gaster for food that is later regurgitated and made available for the rest of the colony is called **social stomach**. Honeypot ants are not the only social insects which share food with other individuals of their colony.

Antplants

Apart from the close relationship between ants on the one hand and aphids and scale insects on the other hand, another close **mutualistic** relationship has developed between ants and antplants (**myrmecophytes**). Antplants possess cavities or **domatia** ('little houses'), that are not bored by ants or other animals, but independently formed. Antplants mostly occur in the tropics and belong to various families. *Acacia sphaerocephala* (**Fabaceae**) provides hollow thorns and extrafloral nectaries for ants, as shown in **fig. 4-4.** The relationship between *Kibara sp.* (**Monimiaceae**), the scale insect *Myzolecanium kibarae* (**Coccidae**) and the ant *Anonychomyrma scrutator* is shown in **fig. 3-20**.

Another outstanding example are ants of the genus *Dolichoderus*. They live in domatia inside the tuber of about 80 different species of **epiphytic** antplants of the genus **Myrmecodinae** belonging to the family **Rubiaceae**. This type of antplant, shown in **fig. 3-22**, can be mainly found on New Guinea island. There are a number of advantages of this close relationship between ants and their respective antplants. The antplants provide shelter and protection for the ants. Many antplants release an unpleasant smell of **butyric acid** that might deter birds and other animals from probing for ants inside the antplant. Ants in return, provide nutrients and play an important role for seed dispersal. Seeds of the antplants are collected by the ants and stored in special cavities of the antplant, until a suitable site for 'planting' is identified by the ants. Usually a mature tree is chosen to ensure that the bark doesn't grow much more so that the cast off bark including the attached antplant doesn't fall off. Apart from this, the ants keep the antplant free of weeds and other epiphytes and might defend their antplant against herbivores. Furthermore, the ants dispose of their debris like faeces, dead ants, etc. in 'warty' cavities of the antplant. The nutrients of the decaying debris are incorporated by the antplant. Antplants can be also inhabited by wild honey bees.

Fig. 3-22: A cross-section of the ant-epiphyte *Myrmecodia spp.* shows chambers inhabited by ants of the genus Dolichoderus. See text for more details (reproduced from Gullan, P.J. and Cranston, P.S., 1994)

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