Giant termite workers at the centre of the picture, surrounded by the more heavily pigmented soldiers.

'Some primal termite knocked on wood
And tasted it, and found it good,
And that is why your cousin May
Fell through the parlor floor today.'

Ogden Nash

The queen of a *Coptotermes lacteus* colony dwarfs the dark-coloured king next to her.

Three large *Coptotermes lacteus* female neotenics with a smaller neotenic male just below them in the picture.

Termite colonies — castes of thousands

Not only the parlour floor, but bitumen, plastic- and lead-sheathed telegraph cables, inflated rubber tyres on vehicles, car batteries, and even ivory and billiard balls (not to mention living plants) have variously been nibbled at by northern Australia's giant termite *Mastotermes darwiniensis*.

Increasing development in northern Australia has allowed this species to fully explore its destructive potential on structural timber and other materials. Inhabitants of the southern capitals can be thankful that it occurs almost exclusively north of the Tropic of Capricorn, for it is Australia's most destructive termite.

The primal termite whose descendents caused cousin May's downfall may have closely resembled *M. darwiniensis*, the only surviving species of an ancient family of termites that once lived in Europe and the Americas, but is now confined to Australia. To entomologists, it is as remarkable an animal as the platypus.

How can such an apparently primitive creature be so destructive? And how does the giant termite compare with other species of Australian termites, such as the species of *Coptotermes* that pester man in the southern half of the continent?

The giant termite's large size and reproductive efficiency explain its success: each soft-bodied, whitish termite weighs up to 50 milligrams, and lives in colonies several million strong. It is not hard to imagine the aftermath of a family dinner of a million or so of these organisms!

The CSIRO Division of Entomology in Canberra is undertaking research into the biology, taxonomy, and control of these damaging species. In a major program, the scientists aim at characterizing the different termite caste systems. They have also initiated studies into the use of biological agents, particularly fungal pathogens, against termites.

Dr Tony Watson and his colleagues at the Division have been digging away at colonies of the giant termite for a decade to find out why it is so prolific.

In most species of termite, a single large queen is solely responsible for egg-laying within the colony. Although highly fecund, her capacity is limited; once fully developed, she reaches a maximum egg-laying rate.

Where replacement or secondary reproductive individuals (the so-called neotenics) occur, they commonly develop from the caste known as nymphs. In most cases, only one or a few pairs of these neotenics are able to breed at one time; their presence normally inhibits the development of more neotenics.

In the giant termite and a few other species, however, the scientists have found that members of the sterile worker caste continually develop into neotenics. Only in *M. darwiniensis* can these be present in enormous numbers and, while the fecundity of each individual is low compared with that of a single, swollen queen, their total output can be much greater.

Slavery

Although often called white ants, termites are more closely related to cockroaches. But like ants, some wasps and bees, and other social insects they live in colonies or large family groups — mum and dad and 100, or 10 000, or 1 000 000 kids.

The different social castes in the highly organized colonies are based on a division of labour. Reproduction, feeding, building, and defence are each undertaken by individuals specifically adapted for that function. The workers are the most numerous individuals, followed by the soldiers and, seasonally, the nymphs; the rest are larvae. The original queen and king, or the neotenics that can replace them, rule the colony.

The caste ratios of field colonies of termites are hard to estimate. Dr Watson, Mr Robert Barrett, and Mrs Hilda Abbey maintained a relatively long-lived colony of *M. darwiniensis* brought into the laboratory from the field and found after 18 years that the 8400 termites comprised 5·7% soldiers, 9·6% larvae, and nearly 85% workers. (The colony was ruled by one female and five male neotenics.) Similar ratios were found in several hundred small colonies set up from primary pairs, presumably

The pioneers of giant termite colonies — *Mastotermes darwiniensis* alates.

A pair of neotenics from a giant termite colony.

approximating the proportions in 'wild' colonies.

Far from representing a dictatorship of the proletariat, the workers live in a type of slavery. In most termite species, they do all the building, foraging, provisioning for the colony, tending eggs and larvae, and feeding members of the other castes.

Typically, termite colonies are founded by a single primary reproductive pair — the king and queen. The queen produces chemical substances (pheromones) that, among other things, prevent development of other reproductive individuals. Pheromones are transmitted throughout the colony via the workers who constantly groom her.

The queen commonly remains in the royal cell in the middle of the colony, producing eggs from her huge blimp-like body for workers to relay to the nursery chambers, where eggs hatch into larvae. In some species, she may lay thousands of eggs in a day, while in winter, when termite mounds cool down, she may stop laying eggs altogether.

Soldiers protect the colony. They stand guard at any opening to the nest — foraging tunnels, flight holes, or damaged regions — attacking any intruders that approach the workers, and secreting alarm pheromones to alert the workers to retreat.

While these alarm pheromones cause workers to regain the safety of the nest, they stimulate any soldiers in the region to hurry towards the attacker, and remain outside the colony until all workers have been rescued.

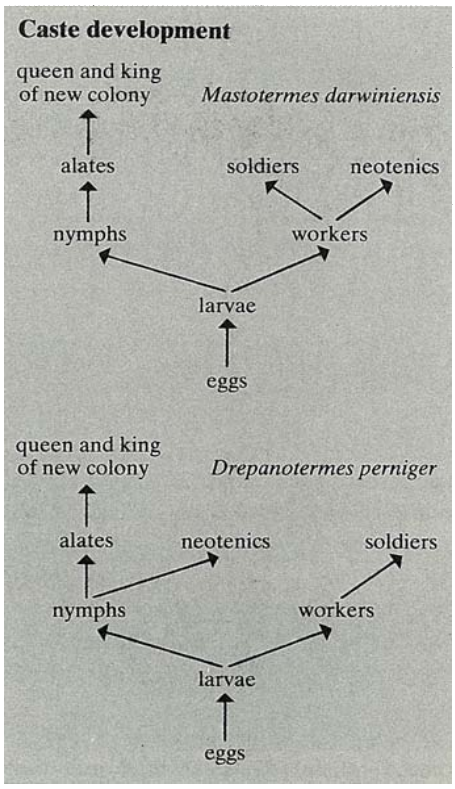
Most soldiers have formidable biting jaws and toxic secretions to pour into the wounds of their victims. Others have developed the toxic secretions into a more sophisticated armoury: sticky substances shot at intruders through a long, hollow 'nose', enmeshing and immobilizing them. Should it not take action against an aggressor, the rear-guard of soldiers backs into the nest behind the workers, battening down the hatches.

Nymphs are the precursors of the royal pair; they metamorphose into winged termites that fly from the nest, settle, and begin new colonies.

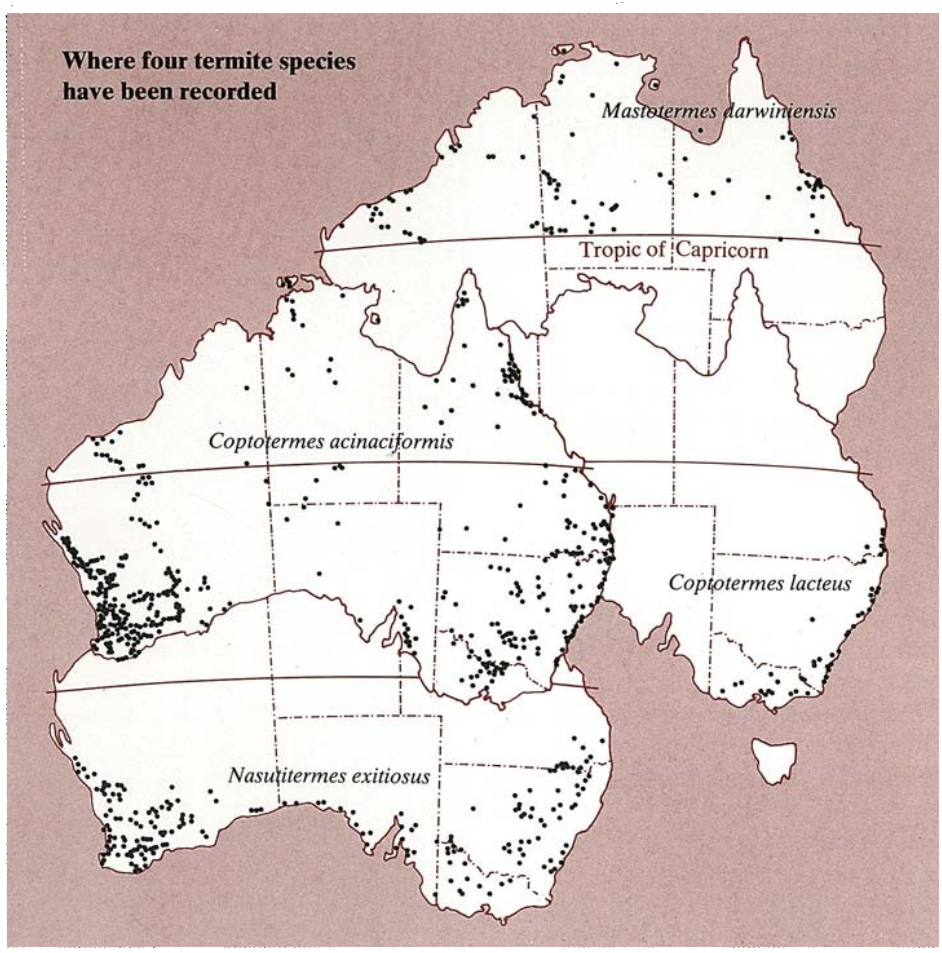
This general model of life in a termite mound has many points of departure among the 300 different species found in Australia. An immense diversity of caste systems exists. Yet, as far as is known, all termite eggs begin as 'totipotent' entities, hatching into larvae that develop into workers, soldiers, or winged reproductive individuals depending on the colony's physiological environment. The queen maintains this environment by pheromone secretions.

Neotenics

About 10 years ago, Dr Watson and his colleagues at the Division began collecting giant termites (*M. darwiniensis*) from Townsville, Qld, so that they could develop techniques for using them in laboratory studies of materials susceptible to the termite.



In *Mastotermes darwiniensis*, reproductive neotenics develop from workers and can be present in very large numbers. More commonly, neotenics develop from nymphs, as in a species of harvester termite (bottom).



The CSIRO scientists soon noticed that some samples of giant termite workers they had taken from the field rarely produced neotenics, although in the absence of the king and queen they could have been expected to produce them readily. Surprisingly, when the researchers added a neotenic to such an orphaned group, many more neotenics appeared.

Subsequent work allowed the researchers to identify the developmental pathway of castes within the species. They found that the eggs hatch into the first larval stage, after which individuals become either workers or nymphs. Nymphs soon develop rudimentary wings, which become full-sized as they mature into winged reproductive termites (called alates) that fly away with the object of starting new colonies.

Mastotermes larvae go through up to six moults before developing into workers, and then undergo an indefinite number of adult worker moults. Workers can develop from any one of these into either presoldiers (then soldiers) or neotenics.

Dr Watson and Mrs Abbey set up cultures in the Division's laboratories in

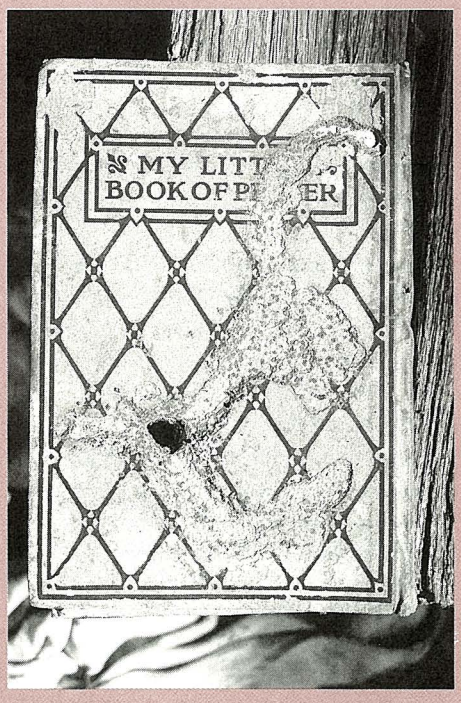
Biological warfare against termites?

Of the 300 species of termite in Australia, only 10–15 are troublesome to man. An integrated pest-management approach to the control of these species requires detailed knowledge of the termites' biology, since only then can we pinpoint their vulnerabilities. Various insecticides (including methyl bromide and chlorinated hydrocarbons) are currently used, but entomologists are attempting to eliminate the use of these by developing more sophisticated methods based on termite behaviour.

For example, the dependence of colonies on pheromones leaves them open to hormone juggling by man. Dr John French of the CSIRO Division of Chemical and Wood Technology in Melbourne conducted laboratory experiments in which several Australian species of termite were treated with synthetic juvenile hormones that caused more workers than normal to develop into soldiers. His results suggested that such hormones might have deleterious effects on the colony's food-gathering efficiency.

However, Dr Lenz showed that simulating natural caste composition and providing a more normal environment decreased the effect of the treatment. This explains why field tests have proved far less successful than the laboratory trials.

Slow-acting poisons have proved more promising. Pest exterminators have long known that if arsenical dust is blown into termite galleries — or termites are dusted and returned to their galleries, which are then sealed — fellow workers groom the dusty termites and carry the poison back to the main nest.



Evidence of a giant termite infestation at Koolpinyah Station, N.T.

In feeding the king and queen, soldiers, and young larvae, the workers contaminate them. Dead termites are eaten by the living (cannibalism sometimes has its evolutionary pay-offs), and soon the arsenic is widely distributed and the entire colony is wiped out. This method can be effective because the termites have plenty of time to distribute the arsenic through the colony before it begins to act. Unfortunately, the treatment is difficult to apply, and finely powdered arsenic is hard to obtain.

Entomologists have been examining methods of biological control as an alternative to chemical control. During the last two decades, various researchers have studied the effects of fungal pathogens on termites. During his stay at the Division of Entomology in 1980/81, Mr Heinz Hanel from Frankfurt, Germany, found that a strain of the fungus *Metarhizium anisopliae* could cripple laboratory cultures of three Australian species of termites — *M. darwiniensis*, *Coptotermes frenchi*, and *Nasutitermes exitiosus*.

Mr Hanel and Dr Watson then set about testing the efficiency of this fungal strain against field colonies of *N. exitiosus*, a well-known southern Australian termite that causes damage to many man-made structures.

Field colonies were infected by fungal particles applied by dusting or spraying colony members, in the mound or away from it at feeding sites. Workers dusted with particles of the fungus were accepted by their fellows.

In a few mounds, the disease persisted for up to 15 weeks, by which time few healthy termites could be found in almost half the infected colonies. However, some colonies continued to survive, although samples of workers taken from them showed high levels of contamination by the fungus.

Mr Hanel hopes to return to the Division to find out what factors are inhibiting complete fungal germination in field colonies.

Preliminary field tests on the use of *Metarhizium anisopliae* for the control of *Nasutitermes exitiosus* (Hill) (Isoptera: Termitidae). H. Hanel and J.A.L. Watson. *Bulletin of Entomological Research*, 1983, **73**, 305–13.

Canberra to study more closely the factors that influence the development of neotenics, particularly in orphaned colonies. Their collections — from near Townsville, Qld, and Darwin, N.T. — came from tree trunks, posts, and 'traps' of perforated 200-litre steel drums filled with bait (delectable tit-bits of timber).

During the experiments, Dr Watson and Mrs Abbey found unexpectedly that orphaned groups of giant termite workers from Darwin behaved differently from those collected near Townsville. Darwin-collected groups readily formed neotenics in the laboratory, whereas Townsville-based groups remained orphaned. Yet both groups produced secondary reproductives when the team added new neotenics.

When neotenics were added to orphaned groups, the response varied according to the circumstances. Older workers responded more readily than younger ones and more than half of the old workers could develop into neotenics within 35 days, the standard test period. The size of the laboratory group was also important. Above a threshold worker population figure of 100–200 individuals, the rate of production of neotenics from workers increased markedly. Mature field-caught neotenic females had the biggest effect — males and newly moulted neotenics were greeted with less metamorphic activity by the group's workers.

Mum and dad and 100, or 10 000, or 1 000 000 kids.

What happens to colonies in the field? Mr Leigh Miller, also of the Division, has found that established giant termite colonies are normally headed by many neotenic reproductives, the original royal pair apparently being short-lived. Most larvae develop into workers; the others become nymphs after the first moult. Some workers become pre-soldiers, then soldiers, the regulatory mechanism being similar to that in other termites: in the case of *Mastotermes*, pre-soldiers develop when soldiers number less than about 5% of the colony.

The rest of the workers continue to moult, and progressively become more likely to turn into neotenics through the influence of the resident neotenics as they age. As the laboratory studies showed, the point at which metamorphosis occurs will depend on the number, sex, and age of the resident neotenics and the size of the colony. But respond the workers eventually do, and finally emerge as neotenics, the natural end-point of development for the majority of workers.

Under normal conditions, and during periods of food shortage, any surplus neotenics are destroyed by their former fellows, the workers. Man has, however, unwittingly provided food parcels to the termite world in the form of railway sleepers and untreated buildings. Natural catastrophes — fire and cyclones — also provide sudden gluts of dead wood: a foodstuff windfall. The termites increase their reproductive rate dramatically by increasing the number of neotenics, and soon the termite village becomes a bustling metropolis.

Radioisotope studies by Mr Bob Paton, formerly of the CSIRO Division of Forest Research but now with the Plant Quarantine section of the Commonwealth Department of Health, have shown that field colonies often occupy areas about 80 metres in diameter. Dr Watson cites a case where insect bait fed to termites in a pine tree near Darwin killed termites in another tree 250 metres away — obviously the two trees formed part of one nest.

Colonizing adaptations

How important are alates in reproduction? In all termite species, the primary king and queen develop from them. The production of new colonies depends on the survival of a few of the millions of alates that leave the nest at certain times of year. After a brief life-or-death flight, they have to find mates before they can begin to construct new colonies, very few of which survive.

You may well ask what possible benefit can accrue to a colony that condemns vast numbers of its inhabitants to death. Entomologists have assumed that the opportunity for genetic recombination involving individuals from different colonies makes the waste worth while, but Dr Watson speculates that alates may represent a colony's excess productivity — packaged for dumping well away from the nest, but still providing the advantage of genetic recombination.

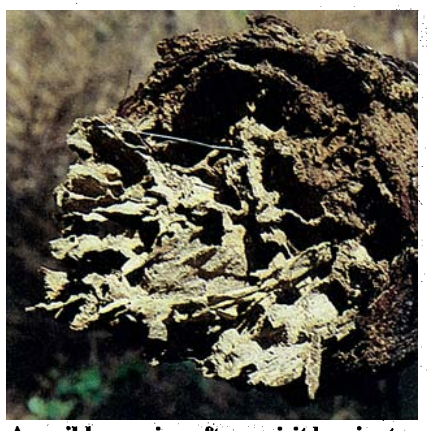
In his studies on Australian species of *Coptotermes*, the Division of Entomology's Dr Michael Lenz discovered a strange phenomenon — breeding neotenics are rarely present in nests of *C. acinaciformis*, *C. frenchi*, and *C. lacteus* in Australia, but the first two species have long been known to form neotenics readily in New Zealand, where they have been introduced. Alates, frequently found in Australian species' nests, have rarely been recorded in New Zealand.

Dr Lenz believes that this is an adaptation of these species to an alien environment. A mature pioneer colony has the potential to send out alates to form new colonies. The success of such a venture, however, requires the saturation of an area with alates from neighbouring colonies over a very brief period. Thus the chances are against the relatively few alates from the pioneer nest finding a spouse (and, consequently, building a nest). Furthermore, the New Zealand environment may not provide the cues that *Coptotermes* colonies need to synchronize production and release of alates.

In recent field studies, Dr Lenz has observed the behaviour of several experimentally orphaned colonies of *C. lacteus* near Canberra and Batemans Bay, N.S.W., and found that they produced neotenics that rapidly began reproducing, enabling the colony to survive. They appeared only when particular nymphal stages were present. Time of year also exerted an effect — of five colonies orphaned in June (winter), only one produced neotenics, even though the appropriate nymphal stages were present.

A South-East Asian species, *C. formosanus*, exhibits an even greater flexibility of colony reproduction. However, many neotenics are the rule in this species. The main nest has 'in-law' satellite nests that can become independent once headed by neotenics from the main nest. After the species is firmly established in a new environment, as in Hawaii, South America, and South Africa, alate flights become the rule, even though many neotenics still inhabit the nests.

Another notorious pest species — the West Indian drywood termite *Cryptotermes brevis* — has successfully invaded new territory, including Australia, with the help of a neotenic-based strategy. (*C. brevis* was the termite detected in several public buildings in Brisbane, including Parliament House, a few years ago. In one of the largest control operations yet mounted anywhere, mountaineers climbed the buildings and draped them with plastic before fumigation. And more recently, in December of last year, a Sydney hotel had to be fumigated with methyl bromide using the same method against the same species.)



A caribbean pine after a visit by giant termites, Darwin, N.T.

A *Coptotermes lacteus* mound near Batemans Bay, N.S.W., in the process of being orphaned. After the researchers find the royal cell near the base of the mound, they remove the queen and replace the broken mound clods, which are then cemented back together by the worker termites.

C. brevis can easily be spread in small pieces of timber (infested furniture, floorboards, and picture frames) often as small groups separated from a king or queen.

Such orphaned groups can produce a large number of neotenics over a short period. After a series of heavy bouts of fighting only one breeding pair remains: not a manifestation of the Cain and Abel myth, but perhaps a literal example of colony adaptation through 'survival of the fittest'. In native Australian species of *Cryptotermes*, which are as a rule confined to natural habitats, neotenics are produced slowly, in small numbers.

Castes-within-castes

Division of labour in termite colonies is often subdivided: at different stages of development, the workers take on specialized tasks in the nest. Dr Watson and Dr Betty McMahan of the University of North Carolina, U.S.A, found that in two species of the Australian harvester termite *Drepanotermes* spp., the large, pigmented mature workers represent the 'heavy machinery'; they repair damage to the

The Brisbane Department of Primary Industries building covered during the *Cryptotermes brevis* fumigating operation.

All of her eggs in one huge basket: the grossly swollen body of the queen of a South African termite species.

mound and venture into the open to gather food for the colony. The smaller, unpigmented, younger workers are the domestics — feeding and tending the eggs and larvae, feeding soldiers, nymphs, and the royal pair, and performing other tasks that keep them near the colony's centre, away from the world outside.

Castes-within-castes occur in other species. For example, *Nasutitermes exitiosus*, a mound-building termite that gnaws through hardwood buildings and fences in suburban and rural areas in southern Australia, has two types of soldier, small (male) and large (female). These soldiers have elongated snouts (the name of the genus comes from *nasus*, Latin for nose) that fire a thread of sticky, toxic material at intruders. The secretion immobilizes its victim, helping soldiers overcome much larger arthropods.

Dr Irmgard Kriston of Wurzburg University in Germany, together with Dr Watson and Dr Tom Eisner from Cornell University in the United States, set up a few simulated 'invasions' of laboratory groups. Using small twirling metal rods, they found that the small soldiers (with longer snouts) approached and examined intruders; if 'attacked' they fired secretions at the enemy. The large, shorter-nosed soldiers followed the advice: 'She who fights and runs away, lives to fight another day'. They showed a strong tendency to retreat, as Dr McMahan had found earlier.

Small soldiers were attracted towards any sticky secretion, grouping around an intruder that had been fired at; large soldiers were repelled. The researchers concluded that the non-combative large soldiers act as messengers, retreating from invasion to raise the alarm in the nest, and to recruit the older, mature workers to repair any damage. As a survival strategy, retreat must have some pay-off. The incidence of large soldiers of *N. exitiosus* varies from one locality to another, and their proportional frequency increases greatly after a colony is orphaned.

Reversionary moulting

The termite caste system demonstrates a number of alternative pathways of development to the one demonstrated in *M. darwiniensis*. One of the most flexible is that of the European termite *Kalotermes flavicollis*.

This species and a few of its allies have a linear developmental pathway — a direct line of development from egg to worker to alate. The larva develops gradually into a 'pseudergate', a worker that can become a soldier, neotenic, or alate, or can remain as a worker. More remarkable is the fact that nymphs with wing buds can revert to wingless workers, which, in turn, can grow a new set of wings when circumstances change. This strange, reversionary moulting has no parallel elsewhere in the insect world.

K. flavicollis, with its flexible, yo-yo pathway of development, lives in small colonies in relatively insecure habitats — a dead branch stub or scar tissue on a tree trunk — in contrast to the stable, long-term nests of species such as *M. darwiniensis*, let alone the temperature-regulated mounds of *Coptotermes* spp. and *Nasutitermes exitiosus*. In their unstable, ephemeral environments, *K. flavicollis* and allied species survive by a 'two-way traffic' caste system of worker-to-winged-reproductive and back again: individuals that would otherwise be committed to becoming alates can return to the worker pool if, for example, climatic conditions become adverse.

The fixed end-points of all termite development are alate (the future king and queen), neotenic, and soldier. Workers, nymphs, and of course larvae all have potential to develop into other castes, but the extent to which they express this potential varies tremendously from one family of termites to another.

The development of *K. flavicollis* illustrates how variable and adaptable termite caste systems can be. They all have one thing in common — an early separation of wingless workers (and soldiers) and winged nymphs, each line retaining in latent form the characteristics of the other. Dr Watson believes that this is the primitive condition in termites.

From the primitive system, two types of termite evolved, one having lesser flexibility associated with large colonies and a relatively stable habitat (as in *M. darwiniensis*, *Coptotermes* spp., and *N. exitiosus*) and the other having extreme flexibility associated with small colonies inhabitating unstable situations, culminating in the worker–alate reverse metamorphosis of *K. flavicollis* and some of its relatives.

Mary Lou Considine

The origin and evolution of caste systems in termites. J.A.L. Watson and J.J. Sewell. *Sociobiology*, 1981, **6**, 101–18.

Development of neotenics in *Mastotermes darwiniensis* Froggatt: an alternative strategy. J.A.L. Watson and H.M. Abbey. In 'Current Themes in Tropical Science. III. Caste Differentiation in Social Insects', ed. J.A.L. Watson, C. Noirot, and B.M. Okot-Kotber. (Pergamon Press: Oxford, in press.)

Caste development in *Mastotermes* and *Kalotermes*: which is primitive? J.A.L. Watson and J.J. Sewell. In 'Current Themes in Tropical Science. III. Caste Differentiation in Social Insects', ed. J.A.L. Watson, C. Noirot, and B.M. Okot-Kotber. (Pergamon Press: Oxford, in press.)

Neotenic production in *Cryptotermes brevis* (Walker): influence on geographical origin, group composition, and maintenance conditions (Isoptera: Kalotermitidae). M. Lenz, E.A. McMahan, and E.R. Williams. *Insectes Sociaux*, 1982, **29**, 148–63.

Neotenic formation in field colonies of *Coptotermes lacteus* (Froggatt) in Australia, with comments on the roles of neotenics in the genus *Coptotermes* (Isoptera: Rhinotermitidae). M. Lenz and R.A. Barrett. *Sociobiology*, 1982, **7**, 47–60.

Reproductive strategies in *Cryptotermes*: neotenic production in indigenous and 'tramp' species in Australia (Isoptera: Kalotermitidae). M. Lenz, R.A. Barrett, and E.R. Williams. In 'Current Themes in Tropical Science. III. Caste Differentiation in Social Insects', ed. J.A.L. Watson, C. Noirot, and B.M. Okot-Kotber. (Pergamon Press: Oxford, in press.)