

SYSTEMATICS AND COMPARATIVE BIOLOGY OF THE HONEYBEES

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INTRODUCTION

Apis mellifera has been a source of wonder and admiration for many centuries within its natural range, including the area that gave rise to western science. As a result it is the most thoroughly studied of all invertebrate animals.

During much of this time, there has been a vague awareness that several closely related species of bees live in Asia, at least one of which could be managed like *A. mellifera*. Nonetheless, until quite recently these other species of honeybees received very little scientific attention and remained poorly known. This situation has been rapidly changing over about the last 15 years, as seen in the publication of a book on *Diversity in the Genus Apis* (Smith 1991a). My purpose here is to brief Caribbean beekeepers and entomologists on these new results in the systematics and comparative biology of honeybees.

Among the estimated 20,000 species of bees is a group of some 1,000 species known as the corbiculate bees (Table 1). The name derives from the pollen basket, or corbicula, a derived character found in females of most species. It is well established that the corbiculate bees as a whole form a natural, monophyletic group, and that each of the four tribes is likewise natural (Michener 1990; Michener et al. 1994). The phylogenetic relationships among the tribes, however, remain controversial. Of the 15 possible cladograms (for four taxa), at least seven have been inferred by various authors, an indication of the unsettled nature of this question (Cameron 1991; Prentice 1991).

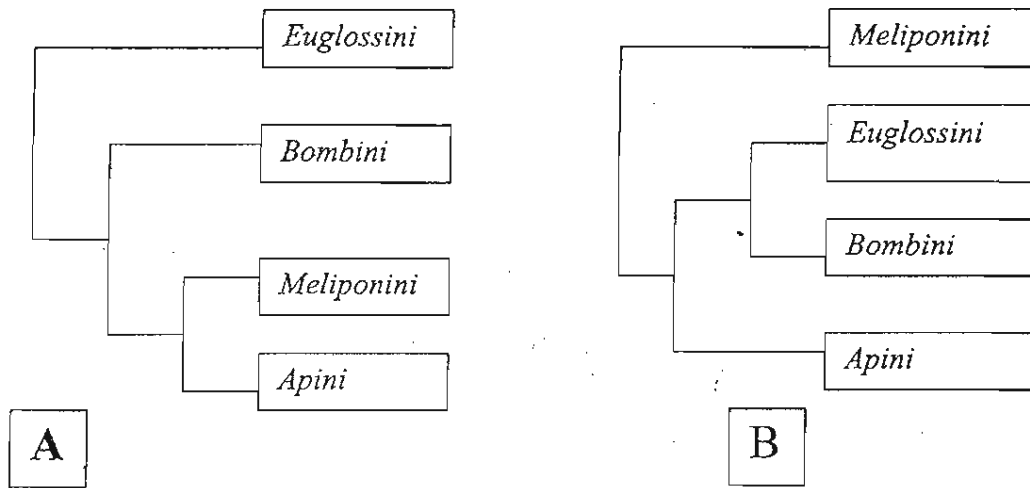
Table 1 Overview of the Corbiculate Bees (*Apidae: Apinae*)

Tribe	Common name	Genera	Species	Distribution
<i>Euglossini</i>	Orchid bees	5	c. 200	neotropics
<i>Bombini</i>	Bumble bees	<i>Bombus</i>	200+	mainly holarctic
<i>Meliponini</i>	Stingless bees	<i>Melipona</i> , <i>Trigona</i> , 6 others	c. 600	pantropical
<i>Apini</i>	Honeybees	<i>Apis</i>	7-10	Asia, Africa, Europe

The two leading candidate cladograms (Fig. 1) show why this question is of interest. The stingless bees (*Meliponini*) and honeybees (*Apini*) are unique among bees in the sophisticated, highly derived nature of their social organization, many features of which are shared between the two groups (Michener 1974). Is this similarity due to recency of common descent, or did they

evolve their social organization independently of each other? If the two tribes are sister-groups, as in cladogram A, similarity through common descent is supported. If, on the other hand, one or the other is more closely related to a less highly social tribe, as in cladogram B, independent evolution is much more likely. And if subsequent results uphold this latter hypothesis, it will raise a second very interesting question: Is there something in the shared features of the corbiculate bees that predisposes them toward the evolution of a highly social way of life? These questions remain very much open at this time.

Figure 1 The two most widely supported cladograms of the tribes of corbiculate bees (*Apinae*)



A. Inferred by Michener (1944, 1990) and Prentice (1991). B. Inferred by Winston and Michener (1977) and Kimsey (1984).

All species of honeybees share or are believed to share a number of striking features, including the following (Seeley 1985; Winston 1987):

- Large colonies
- A well-defined caste system, in which queens and workers are physical distinct and workers are relatively uniform
- A reproductive monopoly by the single queen
- Foundation of new colonies by swarming
- Mating high in the air, the queen typically mated by several males (Oldroyd et al. 1995, 1997)
- Well-developed chemical communication among nestmates, including prominent queen and alarm pheromones
- Recruitment to food sources by means of communicative dances
- Two-sided vertical wax combs

- Sting autonomy, due to strongly barbed sting lancets
- Venom of moderate toxicity, with an LD₅₀ close to 3 mg/kg for mice (Schmidt 1995).

About half of these features are also usual in stingless bees.

The honeybees are readily divided into four distinct groups (Table 2), each with very broad geographic distribution.

The dwarf honeybees have relatively small colonies, as well as small individual body size. The nest consists of a single comb, often no larger than a human hand with the fingers spread, and is typically found in relatively dense, shrubby vegetation. These bees are distributed across south Asia from the Greater Sunda Islands to the Persian Gulf (Fig. 2).

The giant honeybees have larger colonies and much larger individual body size. Workers are about twice as long as those of dwarf honeybees and about six times as heavy. The nest consists of a single comb, often impressively large. The giant honeybees occupy a range across south Asia comparable in size to that of the dwarf honeybees, although shifted eastward (Fig. 3).

The two groups of hive bees are intermediate between these two extremes in colony and individual body size. They are most obviously set apart from the dwarf and giant honeybees by their nests, which typically comprise several parallel combs inside a pre-existing cavity. This habit renders them amenable to being kept in artificial nest cavities (hives) and makes beekeeping possible.

Although they are distinguishable for classification purposes, the eastern and western hive bees resemble each other in their main biological features. As a result, much of our considerable knowledge of *A. mellifera* is transferrable to the eastern hive bees. The eastern hive bees extend over a considerable latitudinal range in east Asia and across south Asia (Fig. 2). The natural range of the western hive bees comprises most of Africa and Europe, with some slight penetration of the Mideast. And, as the favoured bee of beekeeping, it has been carried by humans virtually throughout the tropics and temperate zones of the world.

HOW MANY SPECIES ARE THERE?

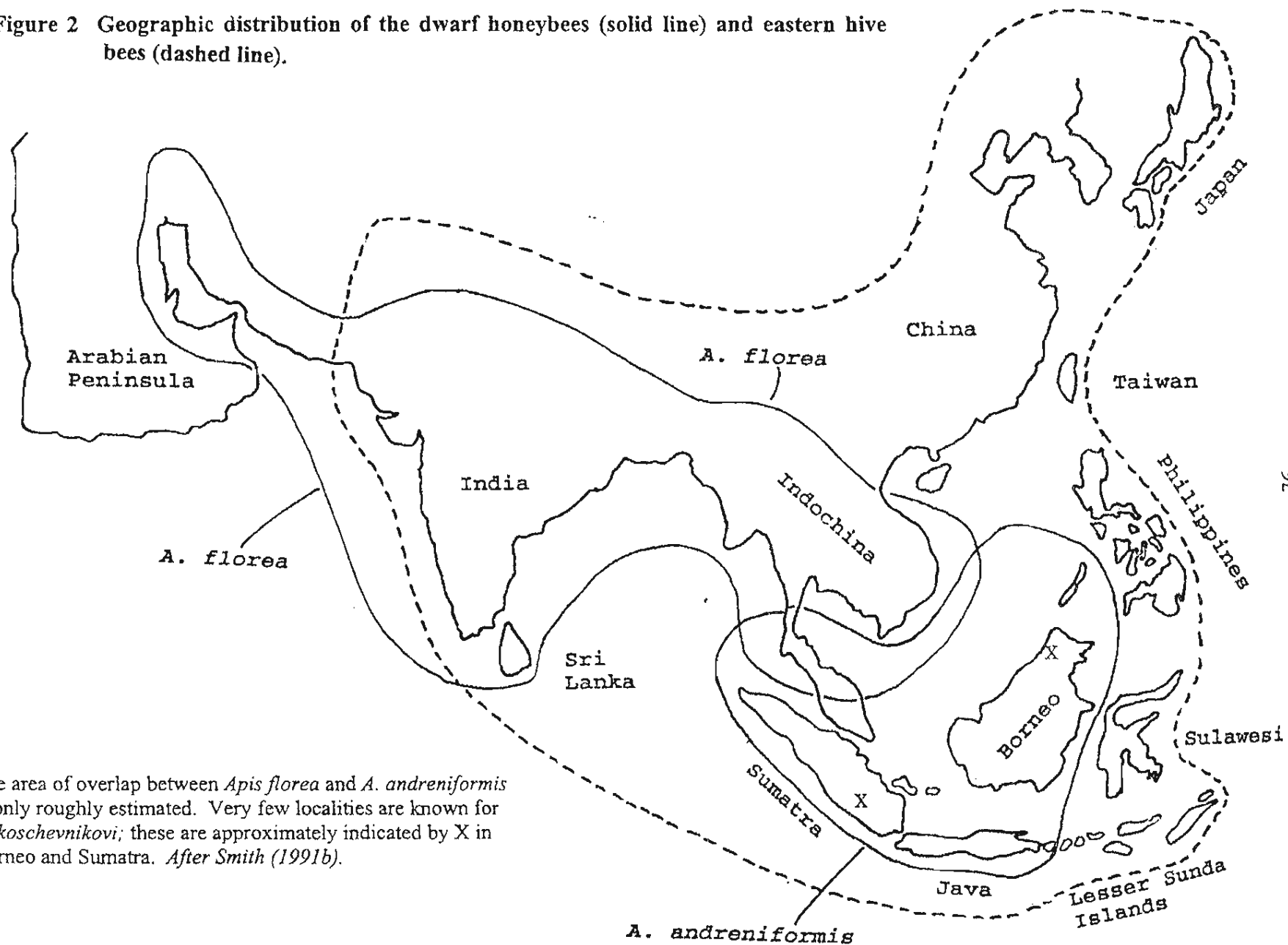
How many species of honeybees are in existence today? The answer to this question can certainly be known, as honeybees are conspicuous and fairly easily collected wherever they are found, unlike many groups of insects with secretive, solitary habits and a great many hidden species.

The traditional view that there are exactly four species (Table 2) was set forth more than a century ago and until recently almost universally accepted (Alexander 1991a; Otis 1991). In a sharp departure from this, Maa (1953) treated each of the traditional species as a subgenus of at least two species and proposed that there are in total 24 species of honey bees (Table 2).

Table 2 Classification of living species of honeybees (genus *Apis*)

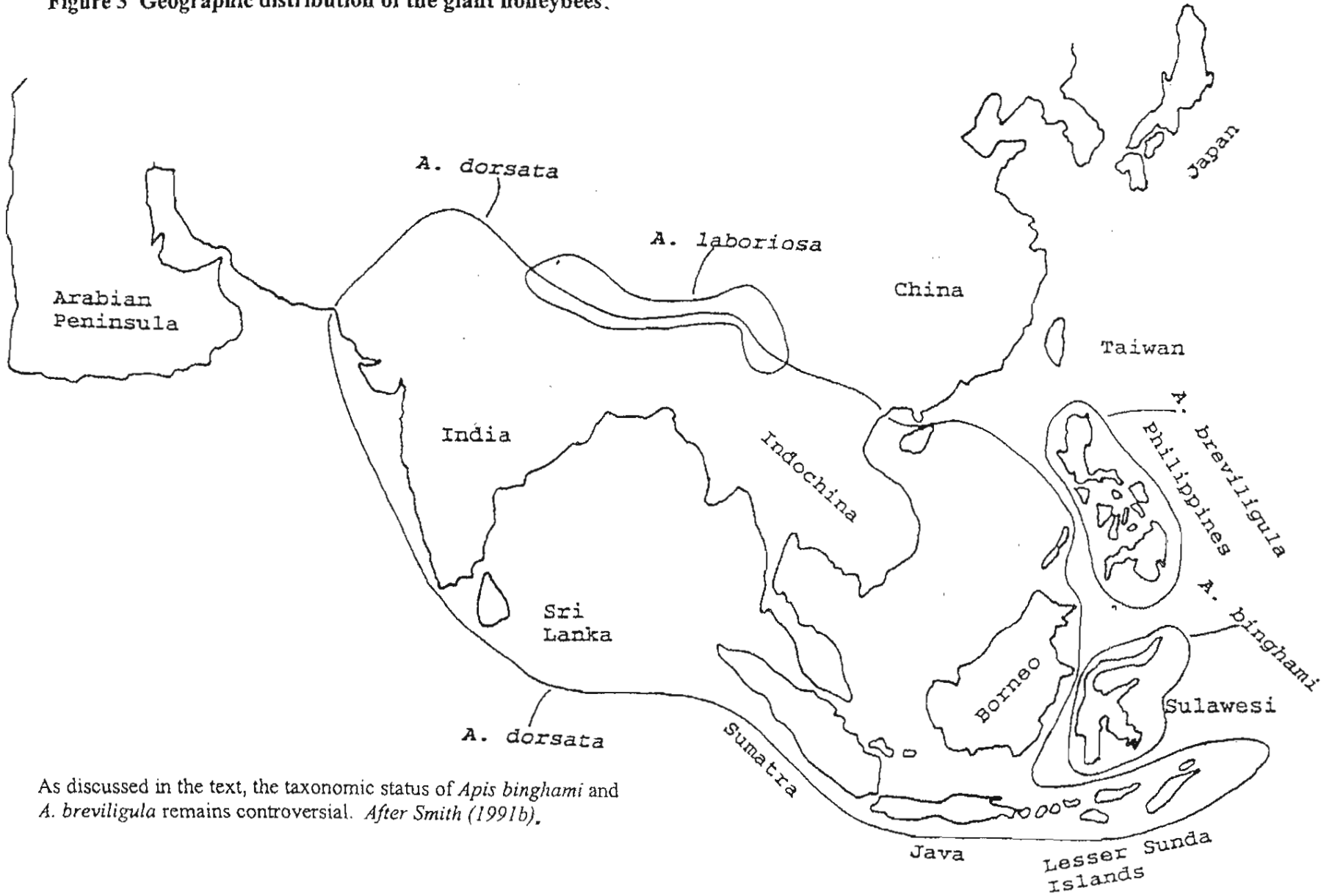
	Traditional	Maa (1953)	Present consensus
Dwarf honeybees	<i>florea</i>	subgenus <i>Micrapis</i> <i>florea</i> <i>andreniformis</i>	<i>florea</i> <i>andreniformis</i>
Giant honeybees	<i>dorsata</i>	subgenus <i>Megapis</i> <i>dorsata</i> <i>binghami</i> <i>breviligula</i> <i>laboriosa</i>	<i>dorsata</i> <i>binghami?</i> <i>breviligula?</i> <i>laboriosa</i>
Eastern hive bees	<i>cerana</i>	subgenus <i>Sigmatapis</i> <i>cerana</i> <i>indica</i> <i>javana</i> <i>johni</i> <i>koschevnikovi</i> <i>lieftincki</i> <i>nigrocincta</i> <i>peroni</i> <i>philippina</i> <i>samarensis</i> <i>vehti</i>	<i>cerana</i> <i>koschevnikovi</i> <i>nigrocincta??</i>
Western hive bees	<i>mellifera</i>	subgenus <i>Apis</i> <i>mellifera</i> <i>adansonii</i> <i>intermissa</i> <i>lamarckii</i> <i>meda</i> <i>remipes</i> <i>unicolor</i>	<i>mellifera</i>

Figure 2 Geographic distribution of the dwarf honeybees (solid line) and eastern hive bees (dashed line).



The area of overlap between *Apis florea* and *A. andreniformis* is only roughly estimated. Very few localities are known for *A. koschevnikovi*; these are approximately indicated by X in Borneo and Sumatra. After Smith (1991b).

Figure 3 Geographic distribution of the giant honeybees.



As discussed in the text, the taxonomic status of *Apis binghami* and *A. breviligula* remains controversial. After Smith (1991b).

Maa's analysis was based on a thorough, competent review of characters. Furthermore, it was reasonable to suppose that such widespread, variable traditional 'species' might in fact each comprise a number of biological species. Nonetheless, Maa's revisionary classification was largely disregarded at the time and for many years afterwards. The reason is not hard to fathom. Although the dwarf, giant and eastern hive bees had not been very thoroughly collected or studied, this was by no means the case with the western hive bees. It was already known at the time of publication that several of Maa's 'species' of western hive bees interbred readily and therefore were not separate species. The traditional view is represented as recently as Ruttner's (1987a, 1987b, 1988) authoritative treatise on honeybee diversity. In this, Ruttner admitted that *A. laboriosa* might be a separate species, but otherwise he held to the four-species scheme. As a specialist in the microtaxonomy of *A. mellifera*, Ruttner had presumably come to have little faith in Maa's species classification as a whole.

However, an upswing of interest in the comparative biology of Asian honeybees, beginning in the 1970s, has called the traditional classification into question. Studies of living honeybees in their native habitat have emphasized diversity within each of the three groups of Asian bees. In addition to contributing new, behavioural-ecological taxonomic characters, this has brought about a new assessment of the physical characters utilized by Maa (1953) and earlier authors and a search for new physical characters. These latter include details of the internal anatomy, almost for the first time. In addition, the new techniques of chemical taxonomy have been brought to bear on the within- and between-species diversity of honeybees.

The result has been intriguing. The emerging consensus on the classification of honeybees is summarized in Table 2. Let us briefly review each of the four groups in turn, from the least to the most problematic.

The traditional view of the western hive bees as a single species, *A. mellifera*, is unequivocally upheld by the array of new results. It might reasonably be supposed that a lineage spread over such a huge geographic and climatic range would fragment into at least a few species, but this has evidently not happened. I am not aware that any important treatment since Maa (1953) has not treated the western hive bees as one species.

In north-eastern Borneo, it had long been noticed that alongside eastern hive bees of normal appearance there existed a peculiar, slightly larger reddish form (Fig. 2) (Rinderer et al. 1989; Tingek et al. 1988). Maa (1953) called this bee *A. koschevnikovi*, but until opinion favoured the view that eastern hive bees might indeed be more than one species, there was no particular search for distinguishing characters. It has now been shown that *A. cerana* and *A. koschevnikovi* are distinguishable on the basis of a chemical character (Gan et al. 1991; Smith 1991b) and the structure of the everted male genitalia (Koeniger 1991; Koeniger et al. 1991).

In addition, an important behavioural character has emerged. Male honeybees (drones) fly out in search of mates only at a certain time of day that is characteristic of the population (Koeniger 1991; Koeniger and Wijayagunasekera 1976). Where *A. cerana* and *A. koschevnikovi* occur together in north-eastern Borneo, their flight times are distinct; *A. cerana* drones fly in early afternoon (almost exclusively between 13:00-14:00) and drones of *A. koschevnikovi* in late afternoon (mainly between 17:00-18:00) (Koeniger 1991; Koeniger et al. 1988). Furthermore, it

is experimentally shown that differences in flight times are due to genetic differences and not to rearing or social environment (Koeniger et al. 1994). Different flight times must reinforce the genetic isolation between the two, working against any latent capacity to hybridize. We may conclude that Maa (1953) was right to recognize the two forms as separate species.

There are suggestions that Maa's (1953) classification of the eastern hive bees may have been correct in one other detail. On the island of Sulawesi, two forms are likewise morphometrically recognizable (Fig. 2), one of which corresponds to Maa's *A. nigrocincta* (Hadisoesilo et al. 1995). This may yet turn out to be a local variant of *A. cerana*. However, the fact that it overlaps in range with apparently normal *A. cerana* suggests that *A. nigrocincta* may be a separate species.

Likewise, the traditional view of the dwarf honeybees as a single species is no longer tenable. Maa's (1953) *Apis florea* and *A. andreniformis* are readily distinguishable on the basis of the male genitalia and hind basitarsus (a secondary sexual character) (Koeniger 1991; Wongsiri et al. 1990; Wu and Kuang 1987). In addition, they can now be separated by allozymes (Gan et al. 1991). Many published field results from '*A. florea*' may in fact come from *A. andreniformis*. The area of sympatry between the two species is only very approximately known (Fig. 2). There is, however, an emerging habitat separation between the two, such that where they are found together *A. florea* occurs in the lowlands, while *A. andreniformis* occurs at higher elevations. Where only one species is found, it tends to show the full altitudinal range of the group, i.e. from sea-level up to about 1,400 metres (Otis 1991).

Unlike in the eastern hive bees and dwarf honeybees, Maa's (1953) putative species of giant honeybees are all readily distinguishable on the basis of external physical features of workers. In particular, a morphometric comparison of Maa's *A. dorsata* and *A. laboriosa* in the area of sympatry demonstrated their distinctness almost 20 years ago (Sakagami et al. 1980). This led Ruttner (1988) to concede that *A. laboriosa* may indeed be a separate species.

Earlier morphometric analyses have since been expanded by Hoshikawa et al. (unpublished) in a study of 112 physical characters from 13 populations, of which 30 characters are informative. These 13 populations separate readily into four clusters entirely consistent with Maa's four species of giant honeybees.

Behavioural comparisons have also contributed distinctions among giant honeybees. Underwood's (1986, 1990) studies of *A. laboriosa* nesting biology leave little room for doubt that it is a separate species from *A. dorsata*. The nesting habits of *A. dorsata* and *A. breviligula* likewise show differences that would seem characteristic of separate species, as discussed below.

However, Maa's classification of giant honeybees is not supported by all of the present evidence. Unlike in the eastern hive bees and dwarf honeybees, the male genitalia are nearly uniform throughout the giant honeybees (Koeniger 1991; McEvoy and Underwood 1988). In addition, the earlier expectation (Sheppard and Berlocher 1989) that the kind of allozyme studies that had so decisively separated *A. koschevnikovi* from *A. cerana* and *A. andreniformis* from *A. florea* would likewise neatly solve the problem of the giant honeybees has not been realized (Gan et al. 1991). However, the uniformity in these characters among Maa's *A. dorsata*, *A. breviligula* and

A. binghami should be considered uninformative, rather than evidence that they constitute a single species. The reason is that some key characters are likewise the same among these forms and *A. laboriosa*, which seems fairly clearly to be a separate species. Variation in cuticular hydrocarbons in giant honeybees (Carlson et al. 1991) is hard to interpret in terms of a species classification.

The lack of geographic overlap between *A. dorsata*, *A. breviligula* and *A. binghami* (Fig. 3) compounds this difficulty. Because no two of these forms are found at any one locality, differences in behavioural-ecological characters such as nesting habit and male flight times (if these are different) are not nearly as decisive as if there was geographic overlap.

Accordingly, the sum of present evidence favours the view that the giant honeybees are at least two species and may be four species (Table 2). This remains the most problematic of the four groups of species. In agreement with Michener (1990), it is my working hypothesis that *A. breviligula* and *A. binghami* are separate species from *A. dorsata*.

I very much regret that in my correspondence with the late T.C. Maa I never thought to ask about the disparity between the present reception of his classifications of western hive bees and of other honeybees. I did not know him nearly well enough to ask how he could have been so astute in treating the dwarf and giant honeybees and yet so mistaken about *A. mellifera*.

COMPARATIVE BIOLOGY

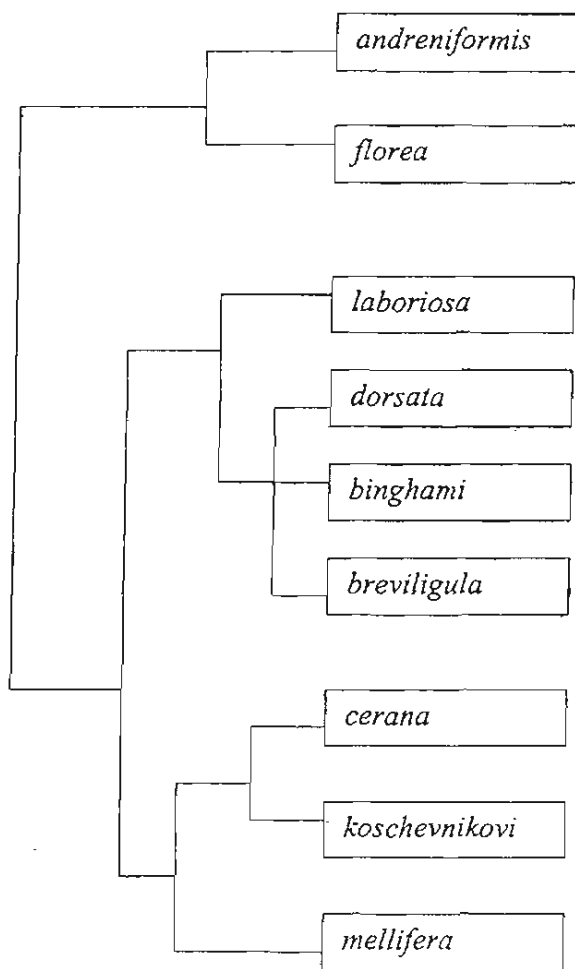
Efforts to solve the species problem in honeybees have gone hand in hand with phylogenetic analyses. A peculiar result of recent studies is that cladograms derived from physical characters (Alexander 1991a, 1991b) and each of three types of chemical characters (Cameron et al. 1992; Kreil 1975; Lockhart et al. 1994; Sheppard and McPherson 1991; Willis et al. 1992) do not agree. However, in those details in which the chemical studies agree with each other, they support the cladogram based on physical characters (Fig. 4) (Engel and Schultz 1997). At present, then, this represents the consensus, with the question left open of how or why types of chemical characters should be so greatly at variance with each other and the physical evidence.

A number of features shared among honeybee species are listed above. With the consensus cladogram as a working hypothesis, we now turn to differences within the genus. After all, as neatly stated by Dyer (1991b): "There is more than one way to be a honeybee."

As indicated above, the most obvious difference is in nesting habit. In this, the three species of hive bees are all very similar, nesting most often in rock and tree hollows in the wild, rarely in the open. In the Philippines I have seen an *A. cerana* colony nesting in an old car tyre with an effectively available volume of no more than three or four litres and in the same area another colony nesting in a building space of about 150 litres. Studies of this species in Sumatra indicate this is about the size range of nest-cavity it utilizes (Inoue et al. 1990). All three species typically construct nests of multiple parallel combs.

Dwarf honeybees have a strikingly different habit. Their nests each consist of a single, more or less exposed comb. By "more or less exposed" is meant that, while they have never been

Figure 4 Consensus cladogram of the honeybees



After Alexander (1991a, 1991b) and Engel and Schultz (1997), with further separation of *A. laboriosa* from other giant honeybees.

reported from tree hollows or other cavities, they tend to be built in low, shrubby vegetation where they can be quite inconspicuous. The comb is small, approximately the size of a human hand with the fingers spread. Its main peculiarity is a horizontal platform at the top, produced by making the uppermost cells extremely deep.

In giant honeybees, also, the nest always comprises a single, exposed comb, although often impressively large (Fig. 5). While the other three groups show only modest, within-group variation in nesting biology, giant honeybees vary in two major ways.

First, in *A. dorsata* and *A. laboriosa*, nests are commonly aggregated. In *A. dorsata*, large trees are the usual nest sites, and they may remain in use by successive generations over many years (Deodikar et al. 1979; Seeley et al. 1982; Starr et al. 1987). In *A. laboriosa*, the usual nest sites are reportedly south-facing cliffs (Roubik et al. 1985; Underwood 1990). The number of active nests in an aggregation can be very impressive. Robinson (1988) includes a photograph of a tree with about 40 *A. dorsata* colonies among its branches, and Dyer (1991b) reports counting 186 colonies in one banyan tree.

On the other hand, aggregated nests have not been reported in either *A. breviligula* (Morse and Laigo 1969; Starr et al. 1987) or *A. binghami* (Otis 1991). Starr et al. (1987) emphasized two other differences in nesting habit that contribute to the view of *A. breviligula* as a separate species from *A. dorsata*: a) *A. dorsata* almost always nests high up, while *A. breviligula* often nests within a very few metres of the ground, and b) *A. dorsata* nests in very open situations, usually on bare, smooth main branches, while *A. breviligula* nests are often more closely surrounded by vegetation.

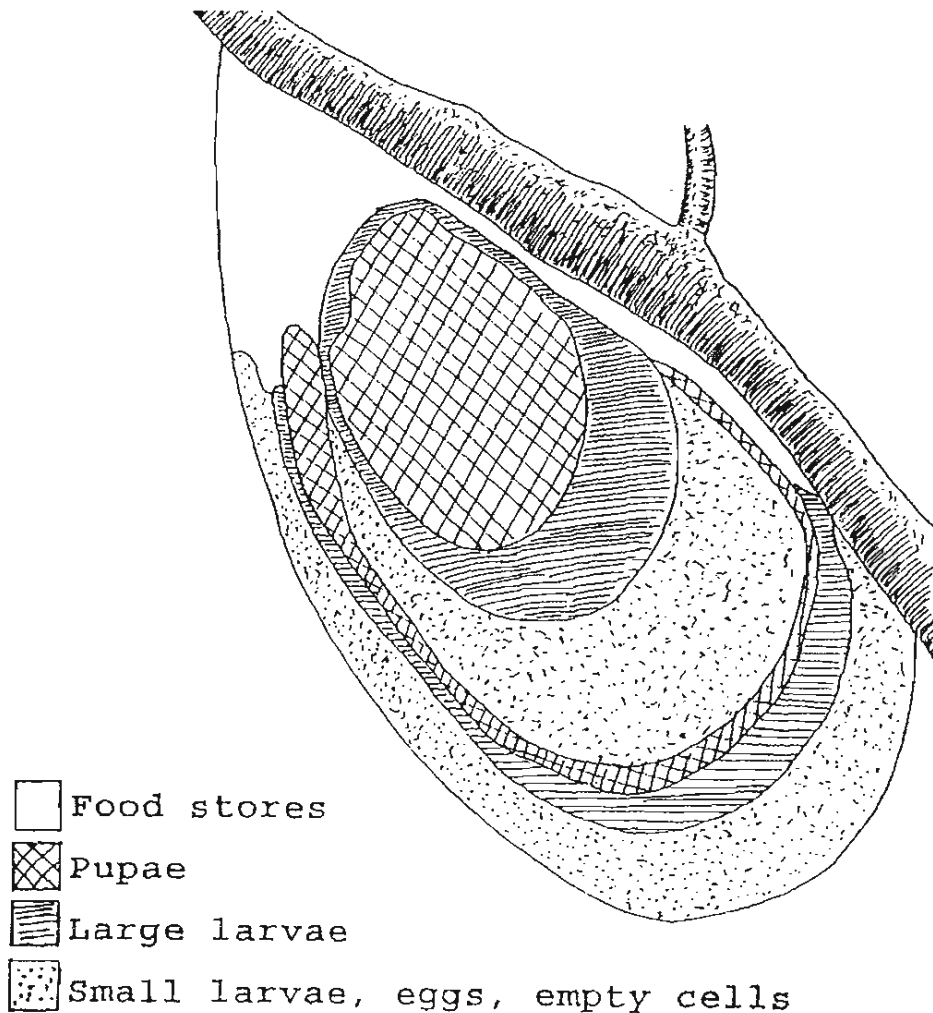
The other important source of variation among giant honeybees is seen in the migratory habits of some populations. In at least parts of its range, migration with seasonal patterns of food abundance appears to be a regular feature of *A. dorsata*, colonies of which may move hundreds of kilometres (Dyer and Seeley 1994; Robinson 1988). *A. laboriosa* has regular altitudinal migrations associated with surviving the winter (Underwood 1990). I am not aware of any reports of migrations by *A. breviligula* or *A. binghami*.

Honeybee species differ in individual body size and number of bees per colony, the two parameters being positively correlated (Dyer 1991b). However, nest size expressed as total number of cells cuts across this trend, such that dwarf and giant honeybees have smaller nests than do hive bees. Mean cells/nest derived from Dyer (1991b) are as follows: *A. florea* 5,040, *A. dorsata* 27,100, *A. cerana* 32,800 and *A. mellifera* 75,200. As a consequence, the first two have more worker bees per cell and presumably a substantially higher worker to brood ratio. In a healthy colony of dwarf or giant honeybees, the comb is literally covered with worker bees most of the time, so that the cells and brood cannot be seen, while in hive bees a part of the comb tends to be exposed at all times.

These differences in nesting habit, nest size, worker body size and number of workers have recently been drawn together and interpreted as alternative strategies for protection of the colony, especially against predators (Dyer 1991b; Seeley 1983, 1985; Seeley et al. 1982). Dwarf honeybees nest inconspicuously in thick foliage and have the smallest workers and colonies. They are thus the most difficult for a predator to find but the easiest to overcome. Giant honeybees usually nest in the open and have the largest workers and colonies. They are easy to find but probably virtually invulnerable to any predator except humans. Hive bees are intermediate in each of these aspects, and are well protected from many predators by their habit of nesting in hard-walled cavities with small entrance-ways.

Differences in nesting habit and colony proportions are also relevant to colony-level energetics. As a rule in insects, including social insects, brood develops more quickly if fed at a higher rate. Similarly, development tends to be more rapid if the brood is kept warmer, which is expected in

Figure 5 Nest comb of *Apis dorsata* from Java, based on a small tree.



The surface area is about 3,000 cm² per side. Traced from a photograph by Flüter (1939).

dwarf and giant honeybees with their higher worker/brood ratios. We might reasonably expect, then, that brood development times would be longer in hive bees.

Against this expectation, average egg-to-adult times for workers are similar among studied species (Dyer 1991b; Dyer and Seeley 1991; Ruttner 1988). The apparent reason for this is that hive bees, including workers, have higher metabolic rates and so work harder at the various aspects of brood care, with worker lifespans accordingly shorter (Dyer and Seeley 1987; Dyer 1991b). In hive bees, both individual workers and the hive as a whole live their lives at a faster pace.

The discovery of the communicative dances of *A. mellifera* was brought to bear relatively early on the comparative biology of honeybees. Lindauer (1956, 1971) studied the dances of *A. florea*, *A. dorsata* and *A. cerana* and found some interesting differences. He supposed *A. florea*, which performs the tail-wagging dance on the horizontal platform above, with the straight run directed toward the food source, to represent the primitive condition in both nest structure and the form of the dance. *A. dorsata*, like *A. mellifera* and *A. cerana*, dances on the vertical comb face. However, Lindauer inferred from his experimental results that *A. dorsata* must be able to see the sun as it dances, in order to communicate effectively, and interpreted *A. dorsata* as evolutionarily intermediate between *A. florea* and the hive bees in this respect. *A. cerana* does not qualitatively differ from *A. mellifera* in its communicative dances, although the code by which the duration of the tail-wagging dance translates into distance of the food source is not the same (Dyer 1991a; Dyer and Seeley 1991; Lindauer 1956).

More recent studies corroborate Lindauer's findings as a first approximation, while revealing new complexities (Dyer 1987, 1991a). *A. florea*, for example, continues to forage and recruit on overcast days, apparently orienting to the (unseen) position of the sun with the aid of learned landmarks. Similarly, *A. dorsata* is not obliged to see the sun during every dance in order to communicate effectively. *A. dorsata* and *A. breviligula* workers often forage on moonlit nights (Dyer 1985; personal observation), and the former have even been observed dancing on such occasions, apparently orienting to the present position of the sun behind the Earth (Dyer 1985, 1991a).

These observations give evidence of sophisticated information processing in these supposedly primitive honeybees, including the ability of the brain to track the changing position of the sun, already known in *A. mellifera* and *A. cerana*. Accordingly, they weaken the hypothesis that *A. florea* resembles the ancestral honeybee in its communicative dances.

SPECIES DIVERSITY AND BEEKEEPING

It is appropriate in these proceedings to end with a few remarks on the economic implications of differences between honeybee species. Only one species, *A. mellifera*, has been introduced into our hemisphere, and this is unlikely to change. However, in much of populous south Asia dwarf honeybees, giant honeybees and eastern hive bees are found together, and in much of this area *A. mellifera* has been added.

Where two or more species are available for exploitation, two economic questions arise. The first is that of honey hunting versus beekeeping, a manifestation of the very old dichotomy between hunting-gathering and farming. Honey hunting is the practice of driving off or killing the adult bees of a wild colony and taking the combs for extraction of honey and sometimes wax. This is an ancient activity (Crane 1975), which continues in south Asia in the primitive fashion.

The preferred prey of honey hunters are giant honeybees, whose very large combs hold much more honey than those of either dwarf or eastern hive bees. And, especially where nests are aggregated, they are undoubtedly much easier to locate. They are also much more dangerous, but the competent use of fire and smoke apparently make the risks manageable. In remote areas

of the Philippines I have often met itinerant honey hunters who earn part or most of their livelihood in this way from *A. breviligula*.

Honey hunting requires virtually no inputs except for labour, and the returns can be very rapid. And like most hunting, and unlike most farming, the techniques to get started are relatively simple and can be learned quickly. (These proceedings will be read by several Professors of Apiculture with advanced degrees in the subject; I have never met anyone with even a diploma in any aspect of hunting.) Against these advantages, honey hunting is labour-intensive, destructive of individual colonies, and, if done well, damaging to honeybee populations and inherently unsustainable. For a similar view of stingless-bee honey hunting, see Kerr et al. (1994).

Beekeeping, in contrast, has been a relatively sophisticated activity for some centuries (Townsend and Crane 1973; Crane 1975), and we may safely predict that it will gain in importance in south Asia as honey hunting declines. Only the eastern and western hive bees are kept. As far as I know, none of the various experimental attempts to manage captive colonies of dwarf and giant honeybees could be described as successful.

This brings us to the second economic question: Does the future of Asian beekeeping lie with the native eastern hive bees or the introduced *A. mellifera*? There are clear indications that beekeepers themselves increasingly favour *A. mellifera*. In Thailand, for example, *A. mellifera* has been the predominant species of beekeeping since about 1980, reversing *A. cerana*'s earlier position (Akranakul 1987; Wongsiri 1989; Wongsiri and Tangkanasing 1986). And I have seen a number of Philippine beekeepers of my acquaintance change their preference from *A. cerana* to *A. mellifera*, but none in the opposite direction.

The reason is explicitly stated by beekeepers. *A. mellifera* has the potential to yield much more honey and more wax per colony than does *A. cerana*. Against this factor, the small farmers who could benefit most from keeping bees as a sideline can often not afford the inputs for *A. mellifera*-keeping or at least cannot afford to fail. And for a beginner the chances of failure are rather high. An *A. cerana*-yard can be begun on a small scale with virtually no capital. Moreover, if the main intended benefit is increased seed-set from pollination, rather than honey and wax, then the greater stores laid in by *A. mellifera* are at most a secondary factor. As far as I know, neither bee has been shown to be the better pollinator of any south Asian crop.

As seen in Table 3, there are other factors to consider, some favouring one species and some the other. My own view at this time is an uncommitted one. I certainly do not concede that the question has been settled in favour of *A. mellifera* as the species for Asian beekeeping. The possibility must be entertained that the future of sophisticated, capital-intensive beekeeping lies with *A. mellifera*, while those keeping bees on a small scale and for other activities will do better with *A. cerana*.

An important reason for withholding judgement is that the two species have not been properly compared. Table 3 is more a reflection of our ignorance than of scientific knowledge. Research in China (Wongsiri et al. 1986), India (Akranakul 1987) and Thailand (Wongsiri 1989; Wongsiri and Tangkanasing 1986; Wongsiri et al. 1987) on methods in keeping *A. cerana* has produced impressive results, but it is still very small-scale beside the several research institutes

in various parts of the world devoted to *A. mellifera*. In addition, the genetics and breeding of *A. mellifera* have long been a sophisticated enterprise comparable to livestock breeding (Rothenbuhler et al. 1968; Cale and Rothenbuhler 1975). There has been very little attempt to similarly exploit genetic variation in *A. cerana* to breed for desirable features.

Table 3 Relative advantages of *Apis cerana* and *A. mellifera* for beekeeping in south Asia

Favouring <i>A. cerana</i>	Favouring <i>A. mellifera</i>
Colonies available in the wild	Forms larger colonies, stores more honey and pollen
Better adapted to the local climate	Less given to swarming and absconding
More resistant to parasites and disease	Less aggressive, easier to manage
Less demanding in hive specifications	Better known biologically

(The *A. mellifera* are presumed to be Italian bees (*A. mellifera ligustica*) or another relatively docile temperate race.) Based on various sources cited in text and personal observations.

SUMMARY

The honeybees (genus *Apis*) are a natural group of highly social bees native to the Old World. Together with the orchid bees (*Euglossini*), bumble bees (genus *Bombus*) and the highly social stingless bees (*Meliponini*), they form a distinctive natural group of major ecological impact. The phylogenetic relationships of these four groups remain controversial, with a great deal of contradictory evidence. Of particular interest is the relationship between the honeybees and stingless bees, as this bears on the question of whether advanced sociality has originated just once or independently twice within the bees.

Apis was until recently thought to comprise four species: the dwarf honeybee *A. florea* and giant honeybee *A. dorsata*, both of south Asia, the eastern hive bee *A. cerana*, of south and east Asia, and the western hive bee *A. mellifera*, native to Africa and Europe and now introduced throughout much of the world.

Recent evidence indicates, however, that there are at least seven and possibly as many as ten species, the giant honeybees being the main area of uncertainty. The very widespread western hive bee is evidently a single species. The phylogenetic relationships between the four groups of honeybees are reasonably well established and serve as a basis for their comparative biology.

The most striking difference within the genus is in nest structure. The dwarf and giant honeybees build a single exposed comb, while the hive bees typically build a set of parallel combs in a cavity. It remains an open question which nesting habit is ancestral for the genus.

Two other areas of interest are the communicative dances peculiar to the genus and the colony-level energetics and ergonomics of the different groups. Recent studies of Asian honeybees have revived the question of the origin and evolution of the dances, with some promising leads.

Some brief attention is given to the relative merits of *A. cerana* versus *A. mellifera* in south Asian apiculture. In the author's view, the conclusion that *A. mellifera* is the bee of the future in south Asia is premature, and more attention to the potential value of *A. cerana* is called for.

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REFERENCES

- Akratanakul P. 1987. Beekeeping in Asia. Rome: FAO
- Alexander, B.A. 1991a. A cladistic analysis of the genus *Apis*. In: Smith D.R (ed.), Diversity in the Genus *Apis*. Boulder: Westview and New Delhi: Oxford and IBH, pp.1-28
- Alexander, B.A. 1991b. Phylogenetic analysis of the genus *Apis* (Hymenoptera: Apidae). Annals of the Entomological Society of America. 84:137-149
- Cale G. H. and Rothenbuhler W.C. 1975. Genetics and breeding of the honeybee. In: Dadant & Sons (ed.), The Hive and the Honey Bee. 20th edn. Hamilton, Illinois: Dadant, pp. 157-184
- Cameron S.A. 1991. A new tribal phylogeny of the *Apidae* inferred from mitochondrial DNA sequences. In: Smith D.R (ed.), Diversity in the Genus *Apis*. Boulder: Westview and New Delhi: Oxford and IBH, pp. 71-87
- Cameron S.A., Derr J.N., Austin A.D., Woolley J.B. and Wharton R.A. 1992. The application of nucleotide sequenced data to phylogeny in the Hymenoptera: a review. Journal of Hymenoptera. Res. 1:63-79
- Carlson D.A., Roubik D.W. and Milstrey S.K. 1991. Distinctive hydrocarbons among giant honeybees, the *Apis dorsata* group (Hymenoptera: Apidae). Apidologie 22:169-181
- Crane E. 1975. The world's beekeeping - past and present. In: Dadant & Sons (eds.), The Hive and the Honey Bee. 20th edn. Hamilton, Illinois: Dadant, pp. 1-18
- Deodikar G.B., Ghatge A.I., Phadke R.P., Mahindre D.B., Kshirsagar K.K., Mural K.S. and Thakar C.V. 1979. Nesting behaviour of Indian honeybees. III. Indian Bee Journal. 39:1-12
- Dyer F.C. 1985. Mechanisms of dance orientation in the Asian honeybee *Apis florea*. Journal of Comparative Physiology. (A) 157:183-198

- Dyer F.C. 1987. New perspectives on the dance orientation of the Asian honeybees. In: Menzel R. and Mercer A. (eds.), *Neurobiology and Behavior of Honeybees*. Berlin: Springer, pp. 54–65
- Dyer F.C. 1991a. Comparative studies of dance communication: Analysis of phylogeny and functioning. In: Smith D.R. (ed.), *Diversity in the Genus *Apis**. Boulder: Westview and New Delhi: Oxford and IBH, pp. 177–198
- Dyer F.C. 1991b. Coadaptation of colony design and worker performance in honeybees. In: Smith D.R. (ed.), *Diversity in the Genus *Apis**. Boulder: Westview and New Delhi: Oxford and IBH, pp. 213–214
- Dyer F.C. and Seeley T.D. 1987. Interspecific comparisons of endothermy in honeybees (*Apis*): deviations from expected size-related patterns. *Journal of Experimental Biology*. 127:1–26
- Dyer F.C. and Seeley T.D. 1991. Nesting behavior and the evolution of worker tempo in three Asian honey bee species. *Ecology* 72:156–170
- Dyer F.C. and Seeley T.D. 1994. Colony migration in the tropical honeybee *Apis dorsata* F. (Hymenoptera: Apidae). *Insectes Sociaux*. 41:129–140
- Engel M.S. and Schultz T.R. 1997. Phylogeny and behavior in honeybees (Hymenoptera: Apidae). *Annals of the Entomological Society of America*. 90:43–53
- Fluiter H.J. de 1939. Beobachtungen an javanischen Hymenopteren. I. *Apis dorsata* F. *Entomologische Mededelingen van de Nederlands-Indië*. 5:45–49
- Gan Y.Y., Otis G.W., Mardani M. and Tan S.G. 1991. Allozyme diversity in Asian *Apis*. In: Smith D.R. (ed.), *Diversity in the Genus *Apis**. Boulder: Westview and New Delhi: Oxford and IBH, pp. 117–130
- Hadisoesilo S., Otis G., Meixner W. and M. Meixner. 1995. Two distinct populations of cavity-nesting honeybees (Hymenoptera: Apidae) in South Sulawesi, Indonesia. *Journal of the Kansas Entomological Society*. 68:399–407
- Hoshikawa K., Sakagami S.F. and Start C.K. (Unpublished) Systematics of the giant honeybees (Hymenoptera: Apidae: *Apis* (*Megapis*))
- Inoue T., Adri and Salmah S. 1990. Nest site selection and reproductive ecology of the Asian honeybee, *Apis cerana indica* in central Sumatra. In: S.F. Sakagami, R. Ohgushi and Roubik D.W. (eds.), *Natural History of Social Wasps and Bees in Equatorial Sumatra*. Sapporo: Hokkaido Univ. Press. pp. 219–232
- Kerr W.E., Nascimento V.A. and Carvalho G.A. 1994. Can our stingless bees be saved? *Pegone* (4):14–16

- Kimsey L.S. 1984. A re-evaluation of the phylogenetic relationships in the *Apidae* (Hymenoptera). *Systematic Entomology*. 9:435–441
- Koeniger G. 1991. Diversity in *Apis* mating systems. In: Smith D.R. (ed.), *Diversity in the Genus Apis*. Boulder: Westview and New Delhi: Oxford and IBH, pp. 199–212
- Koeniger G., Koeniger N., Mardan M., Otis G.W. and Wongsiri S. 1991. Comparative anatomy of male genital organs in the genus *Apis*. *Apidologie* 22:539–552
- Koeniger G., Koeniger N. and Tingek S. 1994. Crossfostered drones of *Apis cerana* (Fabricius, 1793) and *Apis koschevnikovi* (Buttel-Reepen, 1906) fly at their species specific mating times. *Insectes Sociaux*. 41:73–78
- Koeniger N., Koeniger G., Tingek S., Mardan M. and Rinderer T.E. 1988. Reproductive isolation by different time of drone flight between *Apis cerana* (Fabricius, 1793) and *Apis vechti* (Maa, 1953). *Apidologie* 19:103–106
- Koeniger, N. and Wijayagunasekera H.N.P. 1976. Time of drone flight in the three Asiatic honeybee species (*Apis cerana*, *Apis florea*, *Apis dorsata*). *Journal of Apicultural Research*. 15:67–71
- Kreil G. 1975. The structure of *Apis dorsata* melittin: Phylogenetic relationships between honeybees as deduced from sequence data. *FEBS Letters* 54:100–102
- Lindauer M. 1956. Über die Verständigung bei indischen Bienen. *Zeitschrift für vergleichende Physiologie*. 38:521–557
- Lindauer M. 1971. *Communication in Social Bees*, 2nd edn. Cambridge: Harvard University Press
- Lockhart P.J., Steel M.A., Hendy M.D. and Penny D. 1994. Recovering evolutionary trees under a more realistic model of sequence evolution. *Molecular Biology and Evolution*. 11:605–612
- Maa T.C. 1953. An inquiry into the *tribus Apidini* or honeybees (Hymenoptera). *Treubia* 21:525–640
- McEvoy M.V. and Underwood B.A. 1988. The drone and species status of the Himalayan honey bee, *Apis laboriosa* (Hymenoptera: Apidae). *Journal of the Kansas Entomological Society*. 61:246–249
- Michener C.D. 1944. Comparative external morphology, phylogeny, and classification of the bees (Hymenoptera). *Bulletin of the American Museum of Natural History*. 82:151–326
- Michener C.D. 1974. *The Social Behavior of the Bees: A Comparative Study*. Cambridge: Harvard University Press

- Michener C.D. 1990. Classification of the Apidae (Hymenoptera). University of Kansas Science Bulletin. 54:75-163
- Michener C.D., McGinley R.J. and Danforth B. N. 1994. The Bee Genera of North and Central America (Hymenoptera: Apoidea). Washington: Smithsonian Inst. Press
- Morse R.A., Laigo F.M. 1969. *Apis dorsata* in the Philippines (including an annotated bibliography). Philippine Association Entomologists Monographs. (1): 1-96
- Oldroyd B.P., Smolenski A.J., Cornuet J. M., Wongsiri S., Estoup A., Rinderer T.E. and Crozier R.H. 1995. Levels of polyandry and intracolony genetic relationships in *Apis florea*. Behavioral Ecology and Sociobiology. 37:329-335
- Oldroyd B.P., Clifton M.J., Wongsiri S., Rinderer T.E., Sylvester H.A. and Crozier R.H. 1997. Polyandry in the genus *Apis*, particularly *Apis andreniformis*. Behavioral Ecology and Sociobiology. 40:17-26
- Otis G.W. 1991. A review of the diversity of species within *Apis*. In: Smith D.R. (ed.), Diversity in the Genus *Apis*. Boulder: Westview and New Delhi: Oxford and IBH, pp. 29-49
- Prentice M. 1991. Morphological analysis of the tribes of *Apidae*. In: Smith D.R. (ed.), Diversity in the Genus *Apis*. Boulder: Westview and New Delhi: Oxford and IBH. pp. 51-69
- Rinderer T.E., Koeniger N., Tingek S., Mardan M. and Koeniger G. 1989. A morphological comparison of the cavity dwelling honeybees of Borneo, *Apis koschevnikovi* (Buttel-Reepen, 1906) and *Apis cerana* (Fabricius, 1793). Apidologie 20: 405-11
- Robinson W.S. 1988. Beekeeping with *Apis cerana* in Sri Lanka. Bee World 69:125-30
- Rothenbuhler W.C., Kulinčević J.M. and Kerr W.E 1968. Bee genetics. Annual Review of Genetics 2:413-38
- Roubik D.W., Sakagami S.F. and Kudo I. 1985. A note on distribution and nesting of the Himalayan honeybee *Apis laboriosa* Smith. Journal of the Kansas Entomological Society. 58:746-749
- Ruttner F. 1987a. The evolution of honeybees. In: Menzel R. and Mercer A. (eds.), Neurobiology and Behaviour of Honeybees. Berlin: Springer, pp. 8-20
- Ruttner F. 1987b. Taxonomy of honeybees. In: Eder J. & Rembold H. (eds.), Chemistry and Biology of Social Insects. Munich: J. Peperny. pp. 59-63
- Ruttner F. 1988. Biogeography and Taxonomy of Honeybees. Berlin: Springer
- Ruttner F., Kauhausen D. and Koeniger N. 1989. Position of the red honeybee, *Apis koschevnikovi* (Buttel-Reepen 1906), within the genus *Apis*. Apidologie 20:395-404

- Sakagami S.F., Matsumura T. and Itô K. 1980. *Apis laboriosa* in Himalaya, the little known world's largest honeybee (*Hymenoptera, Apidae*). *Insecta Matsumurana*. (NS) 19:47-77
- Schmidt J.O. 1995. Toxinology of venoms from the honeybee genus *Apis*. *Toxicon* 33:917-927
- Seeley T.D. 1983. The ecology of temperate and tropical honeybee societies. *American Scientist*. 71:264-72
- Seeley T.D. 1985. *Honeybee Ecology: A Study of Adaptation in Social Life*. Princeton: Princeton University Press
- Seeley T.D., Seeley R.H. and Akwatanakul P. 1982. Colony defense strategies of honeybees in Thailand. *Ecological Monographs*. 52:43-63
- Sheppard W.S. and Berlocher S.H. 1989. Allozyme variation and differentiation among four *Apis* species. *Apidologie* 20:419-431
- Sheppard W.S. and McPherson B.A. 1991. Ribosomal DNA diversity in *Apidae*. In: Smith D.R. (ed.), *Diversity in the Genus Apis*. Boulder: Westview and New Delhi: Oxford and IBH, pp. 89-102
- Smith D.R. (ed.), 1991a. *Diversity in the Genus Apis*. Boulder: Westview and New Delhi: Oxford and IBH
- Smith D.R. 1991b. Mitochondrial DNA and honeybee biogeography. In: Smith D.R. (ed.), *Diversity in the Genus Apis*. Boulder: Westview and New Delhi: Oxford and IBH, pp. 131-176
- Starr C.K., Schmidt P.J. and Schmidt J.O. 1987. Nest-site preferences of the giant honeybee, *Apis dorsata*, in Borneo. *Pan-Pacific Entomologist*. 63:37-42
- Tingek S., Mardan M., Rinderer T.E., Koeniger N. and Koeniger G. 1988. Rediscovery of *Apis vechti* (Maa, 1953): the Saban honey bee. *Apidologie* 19:97-102
- Townsend G.F. and Crane E. 1973. History of apiculture. In: Smith R.F., Mittler and Smith C.N. (eds.), *History of Entomology*. Palo Alto, California: Annual Reviews, pp. 387-406
- Underwood B.A. 1986. The Natural History of *Apis laboriosa* Smith in Nepal. MSc thesis, Cornell Univ. 88 pp.
- Underwood B.A. 1990. Seasonal nesting cycle and migration patterns of the Himalayan honeybee, *Apis laboriosa*. *National Geographic Research*. 6:276-290
- Willis L.G., Winston M.L. and Honda B.M. 1992. Phylogenetic relationships in the honeybee (genus *Apis*) as determined by the sequence of the cytochrome oxidase II region of mitochondrial DNA. *Molecular Phylogenetics and Evolution*. 1:169-178

- Willis L.G., Winston M.L and Honda B.M. 1992. Phylogenetic relationships in the honeybee (genus *Apis*) as determined by the sequence of the cytochrome oxidase II region of mitochondrial DNA. *Molecular Phylogenetics and Evolution*. 1:169–178
- Winston M.L. and Michener C.D. 1977. Dual origin of highly social behavior among bees. *Proceedings of the National Academy of Science of the USA*. 74:1135–1137
- Winston, M.L. 1987. *The Biology of Honey Bees*. Cambridge: Harvard University Press
- Wongsiri S. 1989. [*Apis cerana* beekeeping problems in developing countries of Southeast Asia.] *Honeybee Science*. 10:1601–64. [Japanese, with English summary]
- Wongsiri S., Lai Y. S. and Liu Z. S. 1986. Beekeeping in Guangdong Province of China and some observations on the Chinese honeybee, *Apis cerana cerana*, and the European honeybee, *Apis mellifera ligustica*. *American Bee Journal*. 126:748–752
- Wongsiri S., Limbipichai K., Tangkanasing P., Mardan M., Rinderer T., Sylvester H.A., Koeniger G. and Otis G.W. 1990. Evidence of reproductive isolation confirms that *Apis andreniformis* (Smith, 1858) is a separate species from sympatric *Apis florea* (Fabricius, 1787). *Apidologie* 21:47–52
- Wongsiri S. and Tangkanasing P. 1986. *Apis cerana* F. beekeeping in Thailand: Problems and research needs. *Journal of Scientific Research of Chulalongkorn University*. (Bangkok) 11:1–6
- Wongsiri S., Tangkanasing P. and Sylvester H.A. 1987. Mites, pests and beekeeping with *Apis cerana* and *Apis mellifera* in Thailand. *American Bee Journal*. 127:5005–03
- Wu Y.R. and Kuang B.Y. 1987. Two species of small honeybee - a study of the genus *Micrapis*. *Bee World* 68:153–154