

Chapter 1

The Asian Species of *Apis*

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1.1 Introduction

The number of species of honeybees recognised over the last two and a half centuries has varied quite considerably, following the original descriptions of *Apis mellifera* (1758) by Linnaeus and *Apis florea* (1787), *Apis cerana* (1793) and *Apis dorsata* (1793) by Fabricius. In the nineteenth century, Frederick Smith (1854–1871) described some 20 additional species, often based on single specimens; only his taxa *Apis andreniformis* (1858) and *Apis nigrocincta* (1861), however, survived in honeybee systematics. Contemporaneously, Gerstäcker (1863) published the first comprehensive phylogenetic and taxonomic treatise on *Apis*, and reduced all previously described forms (except *A. andreniformis* and *A. nigrocincta*, which he either missed or ignored) to only the original four Linnean and Fabrician species. Although Smith (1865) subsequently presented his case for seven species, the views of Gerstäcker (1863) prevailed into the twentieth century (Koschevnikov 1900–1905; Enderlein 1906; von Buttel-Reepen 1906).

Matters then rested for another half century, until Maa (1953) published an abstruse monograph in which he introduced some 24 species of honeybees within four genera. These taxa have subsequently been almost totally ignored in the apicultural literature, and the historically older views of Gerstäcker (1863) have endured until relatively recently. During the years leading up to the publication of Ruttner's (1988) monograph, a search for East Asian honeybees (probably stimulated by Maa's

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original paper) ensued, with *Apis laboriosa* re-announced (Sakagami et al. 1980), *A. andreniformis* re-established (Wu and Kuang 1986, 1987; Kuang 1983), *Apis koschevnikovi* rediscovered (Mathew and Mathew 1988; Rinderer 1988) and *A. nigrocincta* re-entering the scene (Hadisoeso and Otis 1996). Finally, *Apis nuluensis* was described as a new species (Tingek et al. 1996). When Ruttner (1992) subsequently published his natural history of honeybees, he included *A. laboriosa*, *A. andreniformis* and *A. koschevnikovi* alongside the “traditional” four species. In the most recent taxonomy of honeybees, Engel (1999) applied a phylogenetic species concept and accordingly regarded *A. laboriosa* and *A. nuluensis* as synonyms of *A. dorsata* and *A. cerana*, respectively – a view that has not been widely accepted by apiculturists, who have tended to employ alternate species concepts (that is, either the biological species or the evolutionary species concepts). Even now, the number of recognised species of honeybees remains in a state of flux.

Conceptualisation of species recognition also changed through the centuries, from the Platonic concept, exemplified by Linnaeus, to the slow introduction of the idea of a biological species, developed by Poulton (1908), Rensch (1929) and Dobzhansky (1937) and subsequently widely promulgated by Huxley (1940) and Mayr (1942). Indeed, today there are as many concepts for species recognition as there are putative honeybee species, and the very system by which we recognise biological units in nature is fiercely debated (e.g., Wheeler and Meier 2000). Moreover, honeybee researchers have focussed almost exclusively on the oldest of the currently used species concepts, the biological species concept.

Nonetheless, whether a species is diagnosed by population phenomena (the biological species concept), evolutionary lineages (the evolutionary species concept) or genealogical descent (the phylogenetic species concept), classification still requires that species-specific characteristics be brought to bear in the circumscription of species. Likewise, there have been several phylogenetic analyses conducted (Deodikar 1960; Sakai et al. 1986; Sheppard and Berlocher 1989; Alexander 1991; Garnery et al. 1991; Smith 1991; Petrov 1992; Willis et al. 1992; Engel and Schultz 1997; Engel 1999; Raffiudin and Crozier 2007; cf. Chap. 2), all based implicitly on the correctness of the named species.

Following the non-Linnean views of DuPraw (1964), however, coupled with the idea that sub-specific categories are untenable in a contiguous population (Wilson and Brown 1951), Hepburn and Radloff attempted to bypass the problem of classification by designating statistically defined populations of honeybees under the new coinage of “morphoclusters” (Hepburn et al. 2001a, b, 2005; Radloff et al. 2005a, b, c, 2010). They have since accepted the arguments of Engel (personal communication) that “morphoclusters” are really statistically defined “subspecies” to which they had been inconsistently applying trinomial names. Here, we report the results of a full multivariate morphometric analysis of the Asian species of *Apis* and correct the classification of *Apis* in accordance with the rules of the International Code of Zoological Nomenclature.

The systematics of honeybees has also undergone a paradigm shift as earlier evolutionary taxonomic methods and systems of organisation have become passé, having been replaced by the contemporary emphasis on populations, the statistical

distribution of morphological characters and the reconstruction of evolutionary lineages. Moreover, there has been no diagnostic account of the Asian species of *Apis* since Maa (1953). Here, we present the analyses of the currently recognised species of *Apis*: *A. andreniformis*, *A. cerana*, *A. dorsata*, *A. florea*, *A. koschevnikovi*, *A. laboriosa*, *A. mellifera*, *A. nigrocincta* and *A. nuluensis* (noting that *laboriosa* and *nuluensis* are valid only under the antiquated biological species concept). We combine metrical and descriptive morphological characters, DNA characteristics (cf. Chap. 4), behaviour and nesting (cf. Chap. 6) so as to holistically define honeybee species and more easily identify them, either in an equipped laboratory or under field conditions.

1.2 The Dwarf Honeybees

1.2.1 Identification of *Apis andreniformis* and *Apis florea*

The distinctness of both *A. florea* and *A. andreniformis* as unequivocal, valid biological species is now well established and rests on the cumulative knowledge of the morphology of drone genitalia (Lavrekhin 1935; Ruttner 1975, 1988; Kuang and Li 1985; Wu and Kuang 1986, 1987; Wongsiri et al. 1990; Chen 1993; Patinawin and Wongsiri 1993), differences in nest structure (Thakar and Tonapi 1962; Dung et al. 1996; Rinderer et al. 1996; cf. Chap. 6), chemical profiles of beeswax (Aichholz and Lorbeer 1999, 2000; cf. Chap. 6), morphometrics (Jayavasti and Wongsiri 1992; Rinderer et al. 1995), allozyme polymorphism (Nunamaker et al. 1984; Li et al. 1986; Gan et al. 1991), mtDNA sequence divergences (Smith 1991; Willis et al. 1992; Nanork et al. 2001; cf. Chap. 4), flight (Radloff et al. 2001; cf. Chap. 13), timing of mating flights (Rinderer et al. 1993; Otis et al. 2001; cf. Chap. 8), sexual selection (Baer 2005) and niche differences (Oldroyd et al. 1992; Booncham et al. 1995; Rinderer et al. 2002; cf. Chap. 6). Several of these differences contribute to the complete reproductive isolation between the two species (Koeniger and Koeniger 1991, 2000, 2001; Otis 1991; Dung et al. 1996; cf. Chap. 8).

Unfortunately, accurate identifications of the dwarf honeybees in the older literature are often difficult to assess because the worker bees are morphologically similar and the species are sympatric over a wide area that extends from north-eastern India to Indochina (Otis 1996; cf. Chap. 3). Some of the historical confusion between *A. florea* and *A. andreniformis* stems from the fact that their classification is based on workers, which do not show great morphological differentiation. Moreover, the descriptions and taxonomic keys of Maa (1953) were based on very limited numbers of specimens, and some of the purported differences between the two species become blurred if many workers of a colony are analysed.

The most reliable characteristics to rapidly distinguish *A. florea* and *A. andreniformis* are as follows: in drones, the “thumb” of the bifurcated basitarsus of the

hind leg, which in *A. florea* is much longer than that of *A. andreniformis* (Ruttner 1988); the structure of the endophallus (Lavrekhin 1935; Wongsiri et al. 1990; Koeniger 1991; cf. Chap. 8); the cubital index in worker bees, which, at about 3 in *A. florea*, is significantly less than that in *A. andreniformis*, which is at about 6; the jugal-vannal ratio of the hindwing, which, at about 75 in *A. florea* is greater than that of *A. andreniformis*, at about 65; the abdominal tergite 2, which in *A. andreniformis* is deeply punctate, unlike that in *A. florea*; and the marginal setae on the hind tibiae, which in *A. florea* are usually entirely white, while those in *A. andreniformis* are dark-brown to blackish, in sclerotised, non-callow individuals.

Several subspecies, varieties, and nationes of *A. florea*, first described by Fabricius (1787), have been described over the last two centuries (Engel 1999). *A. andreniformis* was described by Smith (1858) as a species distinct from *A. florea* (Fabricius 1787) but was usually included among the varieties or subspecies of the latter for nearly a century, until its re-establishment as a species by Maa (1953). Although *A. andreniformis* was often considered a subspecies of *A. florea*, no sub-specific taxa have ever been proposed for *A. andreniformis*. Unfortunately, an unspecifiable number of specimens of *A. andreniformis* may have been misidentified as *A. florea* during this period. All named forms were eventually resolved into colour variants from widely separated localities (Dover 1929). Subsequently, Maa (1953) synonymised all previous such taxa of earlier workers (Gerstäcker 1863; Enderlein 1906; von Buttel-Reepen 1906; Cockerell 1911; Dover 1929), and no sub-specific categories of *A. florea* have been proposed since then (Hepburn et al. 2005).

The mistaken notion that abdominal tergites 1 and 2 of *A. florea* are reddish and other segments at least partially reddish, while those of *A. andreniformis* are uniformly black, still permeates the literature. However, an inspection of several hundred workers from several different colonies of each species quickly demonstrates the extreme variation in pigmentation. This precludes these characters as a useful distinguishing trait – a point actually recognised rather long ago (Drory 1888; Dover 1929). Finally, the combs of the two species are very different (Rinderer et al. 1996; cf. Chap. 6). Full bibliographies of the literature on *A. florea* and *A. andreniformis* are given in Hepburn and Hepburn (2005, 2009), respectively; cf. Chap. 20).

1.2.2 *Apis andreniformis* F. Smith (1858)

A. andreniformis, the smallest of the honeybees, has been studied far less than *A. florea*. To date, there has been a single univariate morphometric comparison of *A. andreniformis* from southeastern Thailand and Palawan Island in the Philippines (Rinderer et al. 1995). These two widely separated populations (~3,000 km) differed only in a few characters that related to wing and metatarsal lengths, which indicates that it is likely a very homogeneous species. Likewise, estimates of the mtDNA haplotype divergence within the species was about 2% for *A. florea*

and 0.5% for *A. andreniformis*, indicating rather homogeneous populations in both cases (Smith 1991; cf. Chap. 4).

The only published multivariate morphometric analysis of this species is the recent study of Rattanawanee et al. (2008), who collected 67 colonies throughout Thailand – 30 of which were for morphometric analysis and the remaining 37 for DNA polymorphism. Twenty characters were used to assess morphometric variation. Principal component analysis yielded four factor scores, which, when plotted, formed a single group, supported by a dendrogram generated from the cluster analysis. Using linear regression analysis, Rattanawanee et al. (2008) demonstrated the clinal pattern of morphometric characters, wherein body size decreases from west to east, associated with decreasing altitude, while it increases from south to north, associated with increasing altitude. Genetic variation, however, based on the sequence analysis of the cytochrome oxidase subunit b, yielded two groups – a result taken as tentative, pending more extensive analyses across the whole area of distribution of *A. andreniformis* (cf. Chap. 3).

1.2.3 *Apis florea* Fabricius (1787)

Several univariate morphometric studies on regional or country bases have appeared through the years, but they have not affected the taxonomy of the species. In the first multivariate morphometric analysis of *A. florea*, Ruttner (1988) had only limited material, from geographically non-contiguous regions. Although the data were insufficient for a comprehensive analysis, Ruttner (1988) demonstrated geographic variability and obtained three morphoclusters for *A. florea*. Recently, Tahmasebi et al. (2002) analysed *A. florea* and defined two morphoclusters from a geographical continuum in Iran. Combining their data with that of Ruttner (1988) and Mogga and Ruttner (1988), they also reported three morphoclusters for all *A. florea*; but again, a lack of geographical contiguity applies to these data as well. A multivariate study of the *A. florea* of Thailand has also been conducted (Chaiyawong et al. 2004). The raw data of Ruttner (1988), Tahmasebi et al. (2002), Mogga and Ruttner (1988) and Chaiyawong et al. (2004) were included in a subsequent study in which previous gaps in the distribution had been filled, finally allowing a comprehensive morphometric database for *A. florea* over its entire distribution to be compiled (Hepburn et al. 2005).

Principal component, discriminant and cluster analyses using the single linkage (nearest neighbour) procedure were carried out and produced a dendrogram of three main clusters (Fig. 1.1). Phenetically, cluster 1 initially linked colonies from Myanmar and Thailand, followed by Cambodia and finally Northern Vietnam; cluster 2 initially linked colonies from Oman, North India and Nepal, followed by those from South India; cluster 3 linked colonies from Iran and Pakistan; while clusters 2 and 3 linked colonies from Southern Vietnam (Fig. 1.1).

Radloff and Hepburn (1998, 2000) and Hepburn et al. (2001b) established empirically that the greater the sampling distances between localities, the greater



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