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Biogeography of the dwarf honeybees, *Apis andreniformis* and *Apis florea*

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Abstract – The geographical distributions of the dwarf honeybees, *Apis andreniformis* and *Apis florea*, are defined and mapped. The analysis is based primarily on data in the literature for both species and that on the relevant Quaternary palaeoclimatic data. The dwarf honeybee, *A. andreniformis*, extends from the eastern foothills of the Himalayas eastward to Indochina, Sundaland and the Philippines. *A. florea* extends from eastern Oman into southern Iran, eastwards along the foothills of the Himalayas and abruptly stops in southern Thailand. Because they are only partially sympatric, the palaeoclimatic circumstances under which they may have speciated allopatrically are considered. A common and widespread pre-*florea/andreniformis* split could have occurred in the early Pleistocene followed by the Pre-Pastonian glacial (800–1,300 ka) which could well have provided a substantial barrier to gene flow for the then evolving proto-populations of *A. andreniformis* and *A. florea*.

Apis andreniformis / *Apis florea* / biogeography / Southern Asia / speciation

1. INTRODUCTION

The dwarf honeybees, *Apis andreniformis* and *Apis florea*, are sister species with a partially sympatric distribution in southern Asia. These subtropical and tropical honeybees construct a single comb in the open and are absent from colder climates where the more widespread multiple-comb, cavity-dwelling honeybee species occur. Although their propensity for and frequency of swarming and migration varies regionally, it is almost always associated with the sequence: rainfall > flowering > swarming or migration (Hepburn 2006). Swarming and migration are both resource-

related, seasonal movements of tropical honeybee colonies that maximize the colonization of new areas and provide a spatial re-fuelling cycle that is clearly driven by r-selection (MacArthur and Wilson 1967; Hepburn 2006). That *A. andreniformis* and *A. florea* are only partially sympatric suggests that their current area of overlap is a relatively recent development in a Quaternary context. This in turn suggests an earlier palaeoclimatic separation of the precursor populations of these honeybees followed by speciation.

One still wonders why *A. florea* does not extend southwards into the Malay Peninsula. There is recent data by Hughes et al. (2003) who found a significant transition between northern Indochinese and southern Sundaic (Indo-Malay) avifauna assemblages just north of the Isthmus of Kra in the Thai-Malay peninsula (over which *A. florea* would have to have passed). This area is associated with a change from wet seasonal evergreen dipterocarp

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rain forest to mixed moist deciduous forest north of the Isthmus of Kra. Hughes et al. (2003) also reviewed the climatological and ecological factors associated with the forest types and hypothesized that the avian transition tracks the northern phylogeographical boundary and that hypothetical seaways at the end of the Oligocene could account for the development of both phylogeographical and avifaunal transitions as well. Utilising intraspecific molecular variation in fresh water crustaceans, de Bruyn et al. (2005) provided unambiguous evidence in support of the hypothesis of Hughes et al. (2003). To the extent that these interpretations are sound, they would very conveniently explain why *A. florea* does not occur in tropical evergreen rain forests which extend into Thailand, Myanmar, Cambodia and Vietnam (Hadisoelilo et al. 2008).

The distinctness of both *A. florea* and *A. andreniformis* as unequivocal, robust biological species, now well established, rests on the cumulative knowledge of the morphology of drone genitalia, (Lavrekhin 1935; Wu and Kuang 1986, 1987; Ruttner 1988; Chen 1993; Wongsiri et al. 1996), differences in nest structure (Dung et al. 1996; Rinderer et al. 1996), chemical profiles of beeswax composition (Aichholz and Lorbeer 2000), morphometrics (Jayavasti and Wongsiri 1992; Rinderer et al. 1995; Rattanawanee et al. 2007), allozyme polymorphism (Nunamaker et al. 1984; Li et al. 1986; Gan et al. 1991), mtDNA sequence divergences (Smith 1991), flight mechanics (Radloff et al. 2001), timing of mating flights (Rinderer et al. 1993; Otis et al. 2001), sexual selection (Baer 2005), and ecological niche differences (Oldroyd et al. 1992; Booncham 1995; Rinderer et al. 2002; Takahashi 2006). Several of these differences contribute to complete, prezygotic reproductive isolation between the two species (Koeniger and Koeniger 1991, 2000, 2001; Otis 1991; Dung et al. 1996).

Biogeographical inferences about honeybees have been closely tied to prevailing concepts of species in historical terms as well as with the actual amount of data available at any given time. Indeed, the early literature is entirely typological in approach (Maa 1953) but has

been replaced by the biological species concept (DuPraw 1964; Ruttner 1988). Because early works on *A. andreniformis* and *A. florea* were usually conflated prior to Maa (1953) and perhaps until Ruttner (1988), the biogeographical inferences presented in them are only of historical interest (Hepburn et al. 2005).

Although precursors of contemporary *Apis* species have been described from the Eocene epoch of the lower Quaternary period, recognizably modern honeybees first appear in the Pleistocene (Zeuner and Manning 1976; Engel 1998; Grimaldi and Engel 2005; Engel et al. 2009), so that speciation and radiation of modern *A. andreniformis* and *A. florea* must be considered in a Pleistocene context. Moreover, given the palaeoclimatic history for this period (Zubakov and Borzenkova 1990; Goudie 1992; Sloan et al. 1996; Voris 2000) it is now possible to parsimoniously infer how the distributions of both dwarf honeybee species may have arisen. Here we present new distribution maps for the dwarf honeybees and consider how current distributions might reflect the speciation history of these bees in light of palaeoclimatic change.

2. MATERIALS AND METHODS

The literature on *A. florea* and *A. andreniformis* has been compiled in two recent bibliographies (Hepburn and Hepburn 2005, 2009). All the locality data contained in about 2,100 publications were recorded, their geographical coordinates located and mapped with GIS software. The criteria used for regarding *A. florea* and *A. andreniformis* localities as authentic and used to define distribution are those of Otis (1996): (1) published locality data for *A. florea* for central India and to the west are unambiguous because of the absence of *A. andreniformis*; similarly; (2) published locality data for *A. andreniformis* for Malaysia, Indonesia, Borneo and the Philippines are unambiguous because of the absence of *A. florea*; (3) published locality data for bees unambiguously identified as *A. florea* from *A. andreniformis* subsequent to the clear recognition of two biologically distinct species (Wu and Kuang

1987); and (4) the distribution data of Otis (1996) and Hepburn et al. (2005).

Asia is defined here as the region east of a north-south line through the Ural mountains down to the Arabian sea (Peel et al. 2007). The climatic zones of the region discussed here are those of the Köppen-Geiger climate classification system (Köppen 1936). This system is predicated on the idea that major differences in naturally occurring vegetation accurately reflect the effects of climate and this updated world Köppen-Geiger climate map is freely available electronically in the [Supplementary material](#) Section in the paper of Peel et al. (2007) (see [Supplementary material](#)).

While it may seem odd that a climate system should ultimately derive from plant geography, atmospheric scientists have compared contemporary global climate model data with Köppen's maps and found a discrepancy of only about 0.5% (Kalvova et al. 2003). By the same token, Qian et al. (2003) have clearly shown that phytogeographical patterns in eastern Asia are closely related to latitude, which co-vary with climatic variables. The combined results of these biogeographical and atmospheric studies provide a reasonable justification for using the Köppen-Geiger system in biogeographical studies of honeybees (see [Supplementary material](#)).

Map illustrations in most publications on honeybees are routinely delineated by their outer boundary limits as cartoons. This practice is somewhat unfortunate because it predisposes the reader to think that the species is somehow contiguous over the entire area. In actual fact, of the 40 Mkm² of Asian land mass, calculations by Peel et al. (2007) of the relative percentages of Asian land mass occupied by the main climate types yield the following: cold (43.8%), arid (23.8%), tropical (16.3%), temperate (12.3%) and polar (3.8%). The arid, cold and polar climatic regions are essentially devoid of honeybees, thus leaving roughly only an area of, not counting water masses, about 28% (about 11 Mkm²) suitable for sustaining bees. In the distribution maps given here (Figure 1), all known localities from which each species has been collected and reported in the literature (Hepburn and Hepburn 2005, 2009) have been plotted as discrete points. With few exceptions (very probably Afghanistan and possibly Myanmar), the resulting geographical voids may simply indicate that there are few or no dwarf bees in those areas.

Quaternary climatic data relevant to southern Asia were derived from Zubakov and Borzenkova (1990), Goudie (1992), Sloan et al. (1996), and Voris (2000).

A chi-square test based on the frequency distributions for the altitude values for the 117 localities cited in the literature for *A. andreniformis* and 464 localities for *A. florea* was used to compare the altitudinal distributions between species. The test was performed using Statistica (StatSoft 2008).

3. RESULTS

The distributions of the dwarf honeybees, *A. andreniformis* and *A. florea* are shown in Figure 1. The total area occupied by the two species is approximately 8.74 Mkm² of which 59% is purely the domain of *A. florea*, 24% the domain of *A. andreniformis* and the area of sympatry 17%. *A. andreniformis* extends from the foothills of the Himalayas in Sikkim and Bhutan southeasterly through Myanmar, southern China, Thailand, Indochina, then southerly through Malaysia and most of the Sundaland islands and those of Indonesia and on Palawan island in the Philippines. It is primarily a lowland species and the frequency distribution for the altitude values for the 117 localities in the literature show that 87 recorded were found at <500 m elevation, 108 < 1,000 m and the balance > 1,000 m and < 2,500 m.

In the north of the range of *A. andreniformis*, the climate is tropical wet and dry with alternating wet and dry seasons which give way to a tropical wet climate with heavy year round precipitation. A strip of the tropical wet climate also edges the west coast of Myanmar and east coast of Vietnam. Most of the area was once tropical rain forest but tropical dry forest covers central Myanmar and most of central Thailand. *A. andreniformis* is essentially a tropical species of Sundaland, west of the Wallace and Huxley Lines (Figure 1 and [Supplementary material](#)). Of equal interest is where it does not occur: Sulawesi and those islands of the Philippines beyond the Sulu and Celebes Seas; the former is separated from Borneo by the Makassar Strait and the latter

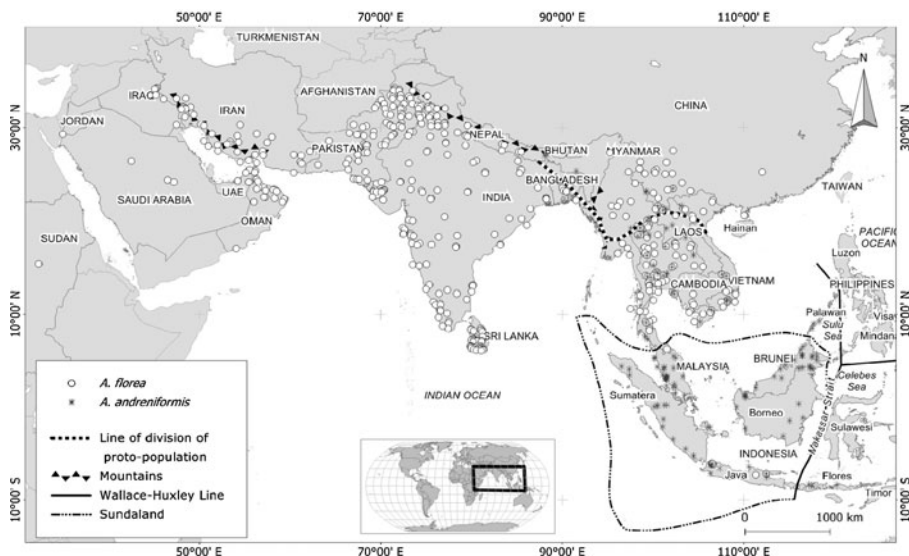


Figure 1. Geographical distribution of *Apis andreniformis* and *A. florea* based on all verifiable published records (Hepburn and Hepburn 2005, 2009).

from Palawan by the Sulu Sea. Both of these seas are over a 1,000 m deep and no land connections existed between them during the Quaternary period (Zubakov and Borzenkova 1990; Goudie 1992; Sloan et al. 1996; Voris 2000).

A. florea occurs naturally on the eastern edge of the Saudi peninsula in Oman and extends across the Persian Gulf into southern Iran and then spreads eastwards below the Zagros mountains, through western Pakistan, then along the foothills of the Himalayas into India, Myanmar, southern China and southeast Asia and abruptly stops in southern Thailand (Figure 1). We suspect that *A. florea* also occurs in Afghanistan. Its climatic range is much broader than that of *A. andreniformis* and includes both desert and semi-arid zones in the west that gradually change to subtropical, tropical dry, tropical wet and dry and tropical wet climate (Figure 1 and Supplementary material).

Like *A. andreniformis*, *A. florea* is also essentially a lowland species and the frequency distribution for 464 localities cited in the literature show that 344 recorded are at <500 m, 402 <1,000 m and the balance

>1,000 m and <2,500 m. Although there is an impression in the literature that *A. andreniformis* is, on average, distributed at somewhat higher elevations than *A. florea* (Wongsiri et al. 1996; Otis 1996) there is no statistically significant difference in their frequency distributions with respect to altitude (Chi-square: $\chi^2=4.5$, 2 d.f., $P=0.1055$).

4. DISCUSSION

Analysis of the geographical distribution of *A. andreniformis* and *A. florea* demonstrates that the former is primarily a tropical and the latter mainly subtropical species. Although both abscond and migrate, their absence from most offshore island groups (Sulawesi and the islands of the Philippines beyond the Sulu and Celebes Seas), and the apparent lack of intraspecific taxa in the two dwarf honeybee species suggests limited dispersal ability (Otis 1996). However, this, coupled with synchronous reproductive seasons across its distribution, further mitigates against regional differentiation of these species into recognizable subspecies/races. Given their present distributions, and the fact that they are sister species, a

parsimonious explanation for their partial sympatry is that a once homogeneous precursor population became climatologically isolated early in a period of Pleistocene glaciation. Speciation then would have occurred allopatrically.

This inference is consistent with palaeoclimatic data for the region and the line of division of the proto-population (Figure 1) appears to be the eastern Himalayas, southward through Nagaland, Manipur, the Chin Hills, the Arakan Yoma in western Myanmar and, further eastwards, the Shan of Thailand and Laos. In subsequent, more recent Quaternary interglacials, the neo-species expanded accordingly to form the relatively small overlap area they currently share. We think that *A. andreniformis* could well thrive in other tropical Asian regions where they do not occur (e.g. Sulawesi, Ceram and Halmahera as well as Irian Jaya and Papua New Guinea), but not in cooler, drier climates to the north and west. On the other hand, *A. florea* appears adapted to far drier climates as indicated by its successful survival where introduced in Saudi Arabia, Jordan and Sudan (Hepburn et al. 2005; Haddad et al. 2008).

Given that *A. andreniformis* and *A. florea* are closely related sister species, and supposing that they diverged from a common Pleistocene ancestor, two obvious hypotheses arise: (1) because it is the more southern species, one could speculate that *A. andreniformis* might have arisen as an isolated island population (e.g. Borneo) followed by its expansion to the mainland during periods of low sea level when the Sunda Shelf was united with the continental mainland; or (2) that a once homogeneous precursor population became climatologically isolated early in a period of continental glaciation in the Pleistocene. Speciation then would have occurred allopatrically, to the west and east of the Himalayan projections into Myanmar, Thailand and Laos. We discount the first possibility on the grounds that during the Pleistocene there were serial glacial and interglacial periods similar to those well-documented for the Quaternary resulting in such time waves of sea level change as to preclude any extended isolation of such an hypothetical island population.

As a third possible explanation of the origin of these two species, Oldroyd and Wongsiri (2006) suggested that speciation between *A. andreniformis* and *A. florea* must have pre-dated island formation because both occur on the mainland and on Java. This suggestion is equivocal, firstly, because the sea surrounding the islands of Sundaland cyclically rose and fell throughout the Pleistocene (Voris 2000). Secondly, *A. florea* has only been reported having been collected once in Java around the port area of Djakarta and on ships in the harbour (Franssen 1931; Maa 1953), which points to an accidental introduction like the recent ones in Sudan (Lord and Nagi 1987) and at Aqaba, Jordan (Haddad et al. 2008).

The mtDNA haplotype divergence between the two species is estimated as 4.6 to 6% (Smith 1991); but within species divergence is about 2% for *A. florea* and 0.5% for *A. andreniformis* indicating rather recent separations in both cases. The chronophylogenetic origins of *A. andreniformis* and *A. florea*, as inferred from nuclear and mitochondrial DNA sequence data by Arias and Sheppard (2005) and Raffiudin and Crozier (2007), differ from that determined proposed by Willis et al. (1992). This suggests that there are fundamental differences in the relative accuracy of the two palaeo-dating methods for defining different regions of mtDNA in time, or to imperfections in the accuracy of both methods. And, indeed, as stated by Arias and Sheppard (2005) "a molecular clock for honey bee mtDNA and the EF1- α intron remains undetermined".

Nevertheless the imprecision in the time scale of the Pleistocene Pre-Pastonian glacial period is sufficiently broad to accommodate either a basal or less proximal position in any of several proposed phylogenetic trees for the evolution of the dwarf honeybees.

We hypothesize that the divergence of *A. andreniformis* and *A. florea* into distinct species can parsimoniously be attached to this time. If we posit a common and widespread pre-*florea/andreniformis* split before the Pleistocene, then there is a convenient barrier caused by the first Pleistocene Barentian (=Pre-Pastonian) Stage glacial period from 800 to 1,300 ka (= Günz Stage of Great Britain, Menapian Glacial Stage

of northern Europe, and Nebraskan Glacial Stage of North America) (Goudie 1992; Gibbard et al. 2007). As the Himalayas extend eastwards, their south-turning extension is the Arakan Yoma mountain ridge, which defines the western border of Myanmar. The arc extends southward nearly 1,000 km from near Manipur in Bengal to southern Myanmar and would have been ice-bound during glacial periods, anyone of which could have provided a barrier for the then evolving proto-populations of *A. andreniformis* and *A. florea*.

Biogéographie des abeilles naines, *Apis andreniformis* et *Apis florea*.

***Apis andreniformis* / *Apis florea* / biogéographie / Asie du Sud / spéciation**

Zusammenfassung—Biogeographie der Zwerghonigbienen *Apis andreniformis* und *Apis florea*. Die geographischen Verbreitungsgebiete von *Apis andreniformis* und *Apis florea* wurden auf der Basis von veröffentlichten Daten zu diesen Honigbienen kartiert (Abb. 1) und im Hinblick auf relevante paläoklimatische Daten aus dem Quartär interpretiert. Das Gebiet von *A. andreniformis* dehnt sich vom östlichen Rand des Himalaya nach Osten bis Indochina, Sundaland und den Philippinen aus. *A. florea* kommt vom östlichen Oman ostwärts über den Iran und entlang der Randgebirge des Himalaya bis in das südliche Thailand vor. Beide sind Arten der Tiefländer und kommen unterhalb von etwa 1,000 m Höhe vor. Die heutigen Honigbienen erschienen erst im Pleistozän, daher muss die Bildung dieser Arten in diesem Zusammenhang gesehen werden. Eine Trennung der prä-*florea/andreniformis* Arten könnte im frühen Pleistozän, vor der Baventischen Eiszeit (800–1,300 ka) stattgefunden haben, die eine Barriere für den genetischen Austausch zwischen den sich trennend entwickelnden Populationen gebildet haben könnte. Ihre gegenwärtige teilweise Sympatrie kann schlüssig damit erklärt werden, dass eine Vorläuferpopulation während einer Eiszeit im frühen Pleistozän klimatisch isoliert wurde und sich daraus eine allopatrische Speziation ergab. Diese Hypothese ist konsistent mit paläoklimatischen Daten; eine Trennung der Vorläuferpopulation könnte entlang dem östlichen Himalaya stattgefunden haben und sich nach Süden in das westliche Myanmar und nach Osten bis nach Thailand

und Laos fortgesetzt haben (Abb. 1). In den folgenden Zwischeneiszeiten hätten sich dann die Arten ausgedehnt und überlappen jetzt in einem kleineren Gebiet.

Daraus, dass *A. andreniformis* und *A. florea* einen gemeinsamen Vorfahren im Pleistozän haben, lassen sich zwei Hypothesen ableiten: (1) weil sie die südlicher vorkommende Art ist, könnte *A. andreniformis* als isolierte Inselpopulation entstanden sein und sich auf das Festland ausgedehnt haben, als das Gebiet des Sundaschelfs mit dem Festland verbunden war, oder (2), eine Vorläuferpopulation wurde während einer Eiszeit im frühen Pleistozän klimatisch isoliert. Die Artbildung wäre dann allopatrisch abgelaufen, in die westlichen und östlichen Ausläufer des Himalaya nach Myanmar, Thailand und Laos. Wir lehnen die erste Hypothese ab, weil es während des Pleistozäns mehrere Schwankungen des Meeresspiegels gab, die eine ausgedehnte Isolierung einer hypothetischen Inselpopulation ausschließen.

Drittens schlugen Oldroyd und Wongsiri (2006) vor, dass die Artbildung von *A. andreniformis* und *A. florea* vor der Inselbildung stattgefunden haben muss, weil beide auf dem Festland und auf Java vorkommen. Dies ist nicht schlüssig, da während des Pleistozäns rund um die Sundainseln der Meeresspiegel wiederholt anstieg und wieder abfiel (Voris 2000), und *A. florea* außerdem nur in der Gegend von Djakarta gesammelt werden konnte (Franssen 1931; Maa 1953).

Wenn wir eine Trennung der prä-*florea/andreniformis* Arten vor dem Pleistozän annehmen, dann gibt es mit der Baventischen Eiszeit eine geeignete Barriere in der Zeit von 800–1,300 ka. Am östlichen Ende des Himalaya biegt die Gebirgskette nach Süden entlang der Grenze von Myanmar ab und formt einen Bogen von Bengalen bis ins südliche Myanmar. Dieser wäre während aller Eiszeiten vergletschert gewesen, von denen jede eine solche Barriere zwischen den sich entwickelnden Arten *A. andreniformis* und *A. florea* gebildet haben könnte.

***Apis andreniformis* / *Apis florea* / Biogeographie / Südliches Asien / Artbildung**

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