Apidologie 36 (2005) 359–376
© INRA/DIB-AGIB/ EDP Sciences, 2005
DOI: 10.1051/apido:2005023

Original article

Apis florea: morphometrics, classification and biogeography[1]

H. Randall HEPBURN[a*], Sarah E. RADLOFF[b], Gard W. OTIS[c], Stefan FUCHS[d],
L.R. VERMA[e], Tan KEN[f], T. CHAIYAWONG[g], G. TAHMASEBI[h], R. EBADI[h],
Siriwat WONGSIRI[g]

[a] Department of Zoology and Entomology, Rhodes University, Grahamstown, 6140, South Africa
[b] Department of Statistics, Rhodes University, Grahamstown, 6140, South Africa
[c] Department of Environmental Biology, University of Guelph, Guelph, Ontario N1G 2W1, Canada
[d] Institut für Bienenkunde (Polytechnische Gesellschaft) Fachbereich Biologie der J. W. Goethe-Universität Frankfurt am Main, Karl-von-Frisch-Weg 2, 61440 Oberursel, Germany
[e] Department of Bio-Sciences, Himachal Pradesh University, Shimla 171005, HP, India
[f] Eastern Bee Research Institute of Yunnan Agricultural University, Kunming, China
[g] Department of Biology, Chulalongkorn University, Phayathai Road, Phathumwan, Bangkok 10330, Thailand
[h] Honeybee Department, Animal Science Research Institute, Karaj, Iran

Received 26 June 2004 – Revised 12 September 2004 – Accepted 13 September 2004

Abstract – Multivariate morphometric analyses were performed on 2923 individual worker bees from 184 colonies representing 103 localities across the full distributional area of *Apis florea* Fabricius 1787 from Vietnam and southeastern China to Iran and Oman (~7000 km). Morphologically *A. florea* is unequivocally separable from *A. andreniformis.* Comparisons of geographically separated *A. florea* populations result in morphoclusters that reflect sampling artifacts. These morphoclusters change clinally with latitude but overlap when the full database is contained in the same principal component analysis. A cluster analysis based on Euclidean distances suggests degrees of affinity between various geographic groupings of *A. florea.* This species occupies a large area that includes rainforests, savannas, subtropical steppes, and semideserts. The seasonality of reproductive swarming is temporally continuous allowing gene flow throughout this panmictic species.

***Apis florea* / morphometrics / distribution / biogeography / swarming / migration**

1. INTRODUCTION

Over the last two centuries, several subspecies, varieties, and nationes of *Apis florea* were described and specimens of *A. andreniformis* identified as *A. florea* (Maa, 1953). The accuracy of identifications of the dwarf honeybees, *Apis florea* Fabricius (1787) and *A. andreniformis* Smith (1858), in the literature prior to 1990 (Otis, 1991) is often difficult to assess because the worker bees are morphologically similar and the species are partially sympatric (Otis, 1997). The mixing of characteristics of the two species is even evident in the monograph of Ruttner (1988). However, the distinctness of *A. florea* and *A. andreniformis* as unequivocal biological species has now been well established based on drone morphology (Ruttner, 1975; Kuang and Li, 1985; Wu and Kuang, 1986, 1987; Ruttner, 1988; Wongsiri et al., 1990; Chen, 1993), nest structure (Dung et al., 1996; Rinderer et al., 1996), morphometrics (Rinderer et al., 1995), allozyme polymorphism (Nunamaker et al., 1984; Li et al., 1986; Gan et al., 1991), mtDNA sequence divergences (Smith, 1991; Nanork et al., 2001;

---

* Corresponding author: r.hepburn@ru.ac.za
[1] Manuscript editor: Stan Schneider

Takahashi et al., unpublished data), and differences in the timing of mating flights (Rinderer et al., 1993). Several of these differences contribute to complete reproductive isolation between the two species (Koeniger and Koeniger, 1991, 2000, 2001; Dung et al., 1996).

Considering infraspecific variation in *A. florea*, Maa (1953) taxonomically synonymized all previous subspecific taxa (Gerstäcker, 1863; Enderlein, 1906; von Buttel-Reepen, 1906; Cockerell, 1911; Dover, 1929). Since then no subspecies of *A. florea* have been proposed (Engel, 1999).

Several univariate regional studies have appeared through the years but have not affected the taxonomy of this species. In the first multivariate morphometric analysis of *A. florea*, Ruttner (1988) had few samples 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) analyzed the *A. florea* of Iran and defined two morphoclusters from a geographical continuum. Combining their data with that of Ruttner (1988) and Mogga and Ruttner (1988), they also reported three morphoclusters for all *A. florea* but a lack of geographical contiguity applies to this database as well.

New collections of *A. florea* from Myanmar, Nepal, Cambodia, Thailand, Vietnam, Iran, Iraq, Afghanistan, Sri Lanka and Saudi Arabia have greatly augmented the database of *A. florea* over a geographical continuum of about 7000 km. The additional, new samples fill gaps to provide a population continuum over the full range of the natural distribution of *A. florea* for the first time. Here we report the results of multivariate morphometric analyses of *A. florea* over its entire natural distribution and compare these results with those obtained from the previous studies. Thus, the morphometric databases for *A. florea* from Iran, India, Thailand and Vietnam were analyzed separately and then conjointly to assess the effects of interlocality sampling distance on morphocluster formation**,** as was previously done for *A. mellifera* (Radloff and Hepburn, 1998) and *A. cerana* (Hepburn et al., 2001b). We also consider whether and how the morphometric data obtained might relate to past classification schemes for *A. florea* (Maa, 1953; Ruttner, 1988, 1992; Engel, 1999). An improved range map showing the distribution of this widespread species is also included.

2. MATERIALS AND METHODS

2.1. Identification of *A. florea* and *A. andreniformis*

The morphometric database currently available for *A. andreniformis* is still too fragmentary for inclusion here. This is unfortunate because 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 limited numbers of specimens and Maa's purported differences between the two species become blurred if all the workers of an entire colony are analyzed.

The most reliable characters adequate for an indentification of *A. florea* and *A. andreniformis* are: the "thumb" of the bifurcated basitarsus of the hindleg of drones of *A. florea* is much longer than that of *A. andreniformis* (Ruttner, 1988); differences in the structure of the endophallus (Lavrekhin, 1935; Wongsiri et al., 1990; Koeniger, 1991); in worker bees, the jugal-vannal ratio of the hindwing of *A. florea* is greater (about 75) than that of *A. andreniformis* (about 65); and the cubital index of *A. florea* (about 3) is significantly less than in *A. andreniformis* (about 6). Abdominal tergite 2 of *A. andreniformis* is deeply punctate, that of *A. florea* not. The marginal setae on the hind tibiae of *A. florea* are usually entirely white, those of *A. andreniformis* dark-brown to blackish in sclerotized individuals. Permeating the older literature is the idea 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. An inspection of several hundred workers from each of several different colonies of each species quickly demonstrates the extreme variation in pigmentation thus precluding this as a useful distinguishing trait, a point recognized rather long ago (Drory, 1888). Finally the combs of the two species are very different (Rinderer et al., 1996). A full bibliography of the literature on *A. florea* is given in Hepburn and Hepburn (2005).

2.2. Geographical distribution

Because of long-standing confusion on whether *A. florea* and *A. andreniformis* are distinct species and because their distributions overlap widely in Southeast Asia (Otis, 1991), precise delineation of the distributions of these two species based on all of the published literature (~ 792 publications on *A. florea* and ~ 101 for *A. andreniformis*, Hepburn and Hepburn, 2005) is somewhat difficult. The most comprehensive and reliable distributional databases for *A. florea* (as herein differentiated) are those of Maa (1953), Ruttner (1988) and Otis (1997).

The criteria for regarding *A. florea* localities as authentic are those of Otis (1997): (1) published locality data for *A. florea* for central India and points west are unambiguous because of the absence of *A. andreniformis*; (2) published locality data unambiguously distinguishing *A. florea* from *A. andreniformis* subsequent to the clear recognition of two biologically distinct species (e.g., Wu and Kuang, 1987); (3) data of Otis (1997); and (4) new distribution records of the authors. Localities were obtained with the appropriate geographical coordinates and plotted using GIS software (Fig. 1, Appendix).

The climatic data was derived from three principal sources: a weatherbase website, http://www.weatherbase.com, Müller (1982) and Troll and Paffen (1980). Data on the seasonality of swarming/migration are from the following: China (Tan Ken, pers. comm.); India (Aggarwal and Kapil, 1988; Deodikar et al., 1977; Millen, 1944; Mehta, 1948; Ghatge, 1949; Soman and Chawda, 1996; Thakar and Tonapi, 1962; Muttoo, 1957; Sihag and Abrol, 1986); Iran (Mossadegh, 1991; Tirgari, 1971); Oman (Dutton and Free, 1979; Free, 1981); Thailand (Akratanakul, 1977); Vietnam (Pham Hong Thai, pers. comm.). Although used implicitly in past publications, the terms macroscale, mesoscale and microscale as used here equate to continental level, country/regional level and localized populations, respectively.

2.3. Morphometrics and statistics

2.3.1. Honeybees

The worker honeybees used for the analyses of *A. florea* in this study derive from: (1) raw data from the Institut für Bienenkunde at Oberursel; (2) new material from Cambodia, Myanmar, Nepal, Thailand and Vietnam (Grahamstown database); (3) the raw data of Bhandari (1983), Sharma (1983), Tahmasebi et al. (2002) and Chaiyawong (2001). Morphometric analyses were performed on 2923 individual worker bees from 184 colonies from 103 localities.

To control subjective variation in measurements among different authors, values from Oberursel were used as a common standard. Thus, (1) the data of Chaiyawong (2001) were standardized for Chiang Mai and Chantaburi, Thailand against Oberursel; (2) the data for Ahwaz, Behbahan, Bushehr, Darab and Bandar Abbas, Iran from Tahmasebi et al. (2002) against Obeursel; (3) data for North India from Bhandari (1983) and Sharma (1983) against Peshawar, Pakistan from Oberursel; and (4) data for Chiang Mai, Thailand and Uminh, Vietnam from Oberursel was used to standardize the Grahamstown database.

2.3.2. Measurements

Twenty morphological characters were used in the analyses; 13 characters in the Ruttner/Oberursel database, 20 characters in the Bhandari/Sharma (provided by Verma) and Grahamstown databases and 17 characters in the Chaiyawong database. The original coded numbers assigned to these characters by Ruttner (1988) and Verma et al. (1989, 1994) are given in rounded and square brackets, respectively, as follows: length of femur (5) [30]; length of tibia (6) [31]; metatarsus length (7) [32]; tergite 3, longitudinal (9) [42]; tergite 4, longitudinal (10) [45]; sternite 3, longitudinal (11) [49]; wax plate of sternite 3, longitudinal (12) [48]; sternite 6, longitudinal (15) [50]; forewing length (17) [5]; wing angle B4 (22) [10]; wing angle D7 (23) [11]; wing angle G18 (25) [13]; forewing-length of radial cell [1]; length of apical position of radial cell [4]; hind wing-length of basal portion of radial vein [20]; length of vannal lobe [29]; length of dark band of 4th tergite [44]; (antenna) length of antennal flagellum [54] and total length of antenna [55]. The Iran database of Tahmasebi et al. (2002) had only 4 common characters (tergites 3+4, longitudinal (9+10) [42+45]; forewing length (17) [5]; LEG length (5+6+7) and wing angle G18 [13]) with the other four databases. Cubital Index (CI) was common to the Oberursel, Bhandari/Sharma and Tahmasebi databases but absent from the Chaiyawong and Grahamstown databases.

2.3.3. Data analysis

Colony sample means and standard deviations were computed for each morphometric character from 15–20 bees per colony. Multivariate statistical analysis of the data included principal components, discriminant and k-means cluster analyses (Johnson and Wichern, 1998; Rao, 1998).

3. RESULTS

3.1. Biogeography

A. florea is extremely widespread, extending some 7000 km from its eastern-most extreme in Vietnam and southeastern China,

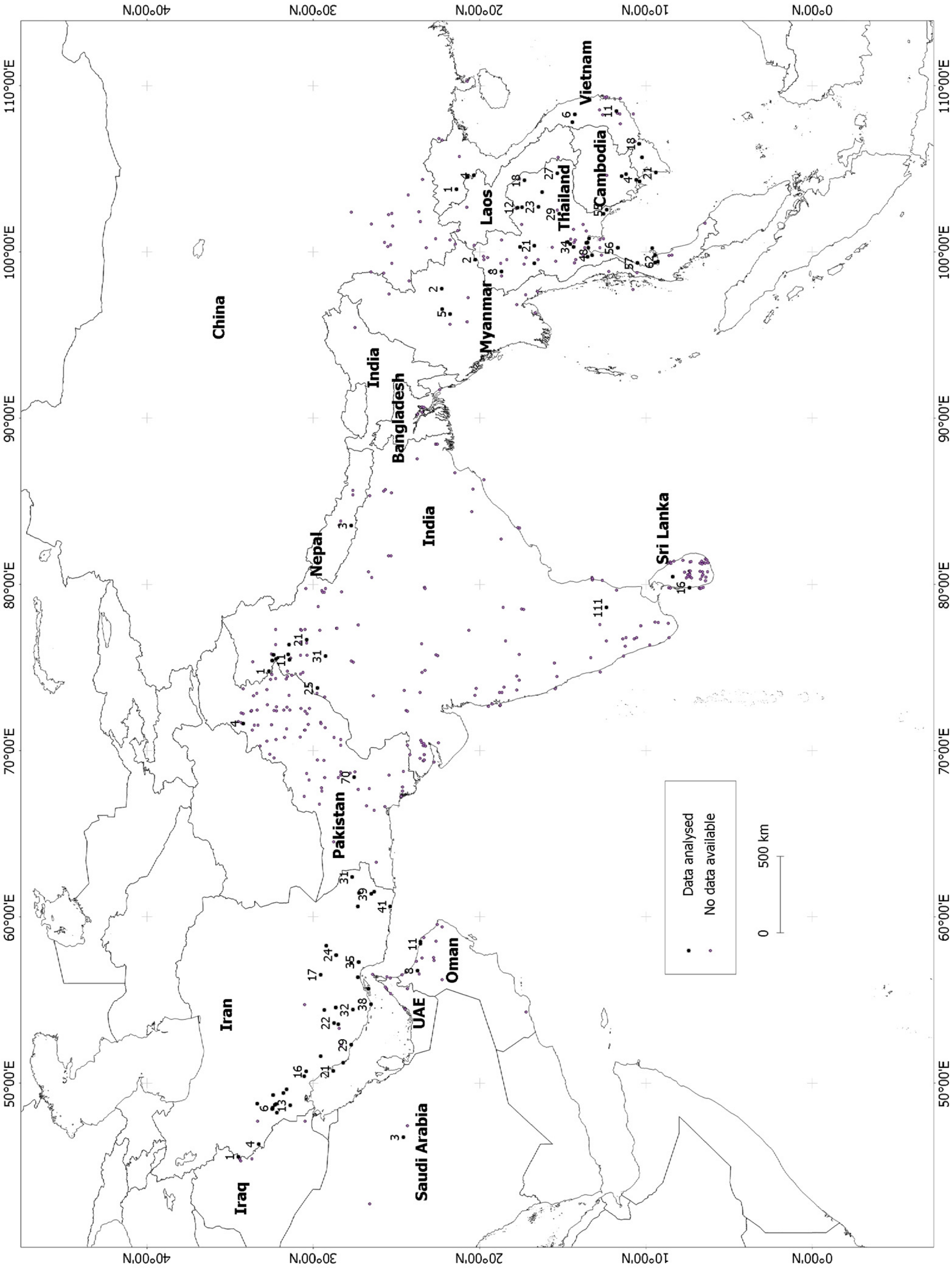

Figure 1. Distribution of *Apis florea.* Localities for which morphometric data are reported are indicated by their country numbers shown in Table I. That the numbers for each country are not sequential derives from the fact that these numbers correspond with the same locality numbers given in Appendix. All other localities are represented by black circles. Not all localities could be shown because the scale used to generate the map resulted in blurred areas because of high sample density. Full references available at http://www.edpsciences.org/apido.

across mainland Asia along and below the southern flanks of the Himalayas, westwards to the Plateau of Iran and southerly into Oman (Fig. 1). This constitutes some 70 degrees of longitude (40°–110° East) and nearly 30 degrees of latitude (6°–34° North). Variations in altitude range from sea level to about 2000 m. *A. florea* has also been introduced in historical times in Saudi Arabia and Sudan, and occurred on Java, Indonesia, up until ~50 years ago.

3.2. Regional mesoscale analyses

3.2.1. Thailand database

A re-analysis of the raw data of Chaiyawong (2001) for the *A. florea* of Thailand (localities 8, 12, 14, 18, 20, 21, 23, 24, 27, 29–31, 34, 44–46, 48, 54–57, 59–62 in Tab. I) was performed using 7 morphometric characters [(5), (6), (7), (9), (10), (17) and G18] common to the databases from Oberursel, Chaiyawong and Grahamstown (62 colonies). Two principal components with eigenvalues greater than one were isolated: PC 1, size-related characters (5), (6), (7), (9), (10) and (17) with component loadings between 0.55 and 0.90 accounted for 57.7% of the variation; PC 2, angle of venation G18 (25) with component loading 0.82 accounted for 16.6% of the variation. The two principal components accounted for a total of 74.4% of the variation in the data. The principal components results revealed one morphocluster with only 2 of the 10 colonies from Ko Samui and Ko Pha-ngan (3% of the total colonies) separated from the principal morphocluster. Another principal components analysis using 17 characters ((5), (6), (7), (9), (10), (11), (12), (15), (17), G18, [1], [4], [20], [29], [44], [54] and [55]) common to Chaiyawong and Grahamstown (58 colonies) gave three principal components with eigenvalues greater than one: PC 1, size related characters ((5), (6), (7), (9), (10), (11), (12), (15), (17), [20], [55]); PC 2, characters [1], [4], [20], [29], [44], [54]; PC 3, angle of venation G18 (25). The plots of PC 1, PC 2 and PC 3 scores again showed a single morphocluster.

3.2.2. India and Sri Lanka databases

A separate analysis of the combined databases for *A. florea* of India from Bhandari/Sharma and Sri Lanka from Oberursel (17 colonies) using 10 common characters [(5), (6), (7), (9), (10), (17), CI, B4, D7 and G18] was performed. Three eigenvalues greater than one were isolated: PC 1, size related characters (5), (6), (7), (9), (10), (17) accounted for 57.1% of the variation; PC 2, angle of venation G18 (25) accounted for 15.8% of the variation; PC 3, cubital index CI accounted for a further 12.2% of the variation. The results of the PC plots showed 2 distinct morphoclusters, a northern group of larger bees and a southern group of smaller bees. A significant correlation between altitude and the first principal component was found (r = 0.78, n = 16, $P = 0.008$).

3.2.3. Iran database

In this study combining the databases from Tahmasebi et al. (2002) and Oberursel (58 colonies), the PC analysis using five common characters ((9+10), (17), CI, LEG and G18) revealed one morphocluster with two indistinct clusters of smaller eastern and larger western bees. The two principal components with eigenvalues greater than one accounted for 72.5% of the variation: PC 1, size related characters [(9+10), (17), LEG]; PC 2, angle of venation [G18 (25)].

3.2.4. Iran, India and Sri Lanka databases

In an analysis combining Bhandari/Sharma and Oberursel databases with that of Tahmasebi et al. (2002) from Iran (61 colonies), the PC results using 4 common characters [(9+10), (17), G18, LEG] showed 3 morphoclusters: a northwestern group of larger bees (Iran); a northeastern group (eastern Iran and N. India) and a southern group of smaller bees from S. India and Sri Lanka (Fig. 2). The northwestern and southern groups are distinct. The first two principal components accounted for 94.2% of the variation in the data: PC 1, size related characters [(9+10), (17), LEG; 70.5%]; PC 2, angle of venation [G18 (25); 23.7%].

The linear discriminant analysis results classified 95.5% of colonies (n = 44) from Iran correctly into group 1 (larger bees) with a posteriori probabilities $P > 0.95$ for 30 colonies, $0.80 < P < 0.95$ for 8 colonies, $0.75 < P < 0.80$ for 3 colonies, $P = 0.56$ for 1 colony, and

Table I. Geographical distribution of *A. florea* by countries, geographical co-ordinates, altitude and number of colonies (n). The sources of the raw data are Grahamstown (G), Oberursel (O), Tahmasebi for Iran (T), Bhandari (1983) and Sharma (1983) for India (B) and (S), respectively and Chaiyawong for Thailand (C)*.

COUNTRY	COORDINATES	ALTITUDE	n	SOURCE
CAMBODIA				
2. Kampong Speu	11.27N 104.32E	16	4	G
3. Takeo	11.00N 104.46E	8	1	G
4. Kampot	10.37N 104.11E	21	1	G
INDIA				
1. Jammu	32.45N 74.55E	327	1	B
3. Hamirpur	32.25N 75.20E	747	1	S
4. Nurpur	32.18N 75.53E	492	1	B
7. Gurdaspur	32.04N 75.28E	264	1	B
9. Hoshiarpu	31.30N 75.55E	316	1	S
10. Una	31.25N 76.15E	420	1	S
11. Karpurthala		224	1	B
21. Kalka	30.20N 76.45E	720	1	S
25. Sriganganagar	29.56N 73.53E	208	1	B
31. Hisar	29.07N 75.46E	212	1	B
111.Yarakapadi	12.18N 78.38E		1	O
IRAN				
1. Ghasre-e-Shirin	34.30N 45.35E	343	1	T
2. Bishe-Moobed	33.18N 48.53E	1444	1	O
4. Mehran	33.07N 46.10E	136	1	T
5. Andimeshk	32.27N 48.21E	136	1	T
6. Dezfol	32.23N 48.28E	148	4	T
7. Lali	32.21N 49.06E	947	1	O
8. Deh Lowran	32.10N 48.46E	169	1	T
9. Shoshtar	32.03N 48.51E	67	1	O
10. Soush	32.00N 48.00E	90	1	T
11. Masjed Suleiman	31.59N 49.18E	337	1	O
12. Ghalieh-Khajeh	31.40N 49.41E	986	1	O
13. Ahwaz	31.17N 48.43E	33	3	O, T
14.Behbahan	30.34N 50.18E	317	3	O, T
16. Dogonbadan	30.21N 50.48E	724	1	T
17. Bidkhan	29.36N 56.30E	2726	1	T
18. Kazeroun	29.35N 51.40E	846	1	O

Table I. Continued.

COUNTRY	COORDINATES	ALTITUDE	n	SOURCE
19. Neyriz	29.14N 54.18E	597	1	O
20. Bam	29.01N 58.04E	1000	1	T
21. Bushehr	28.59N 50.50E	13	2	O, T
22. Fasa	28.55N 53.39E	1336	1	O
23. Darab	28.45N 54.33E	1200	2	O
24. Jiroft	28.41N 57.48E	1750	2	T
25. Jahrom	28.29N 53.32E	1120	2	T
28. Khormoj	28.00N 51.00E	72	1	T
29. Kangan	27.51N 52.07E	156	1	T
30. Rodan	27.50N 57.01E		2	T
31. Saravan	27.45N 62.17E	1163	4	T
32. Lar	27.42N 54.19E	807	2	T
33. Iranshahr	27.12N 60.41E	551	1	T
34. Bandar Abbas	27.12N 56.15E	2	4	O, T
35. Minab	27.07N 57.06E	47	3	T
36. Irandegan	27.03N 61.22E	1148	1	O
37. Gheshm Island	26.48N 55.46E	3	1	T
38. Bandar Lengeh	26.34N 54.52E	0	1	T
39. Kalleh-Gan	26.31N 61.16E	905	1	O
40. Rash	26.13N 61.28E	1700	1	O
41. Basam Chah Bahar	25.16N 60.41E	8	1	O, T
MYANMAR				
2. Mong La	22.07N 97.55E	811	7	G
3. Pyin-oo-lwin	22.05N 96.33E	1070	2	G
5. Mandalay	21.57N 96.04E	80	2	G
NEPAL				
3. Tansen	27.52N 83.32E	1090	1	G
OMAN				
8. Diqal	23.53N 56.54E	119	1	O
10. Qurm	23.36N 58.29E	14	1	O
11. Seeb	23.34N 58.15E	46	1	O
PAKISTAN				
4. Peshawar	34.01N 71.40E	317	2	O

Table I. Continued.

COUNTRY	COORDINATES	ALTITUDE	n	SOURCE
70. Larkana	27.33N 68.18E	44	1	O
SAUDI ARABIA				
3. Riyadh	24.39N 46.52E	6	1	O
SRI LANKA				
7. Anuradhapura	8.18N 80.24E	8	5	O
16. Makandura	7.19N 79.58E	19	1	O
SUDAN				
1. Al Khartum	15.35N 32.32E	377	2	O
THAILAND				
2. Fang	20.05N 99.30E	471	1	O
8. Chiang Mai	18.48N 98.59E	310	4	O, G, C
12. Nong Khai	17.52N 102.44E	168	2	G, C
14. Uttaradit	17.37N 100.06E	246	1	C
16. Udon Thani	17.24N 102.47E	174	1	G
18. Sakhon Nahon	17.10N 104.08E	176	1	C
20. Tak	16.51N 99.08E	111	1	C
21. Phitsanulok	16.50N 100.15E	41	1	C
23. Khon Kaen	16.26N 102.49E	164	1	C
24. Roi Et	16.05N 103.38E	143	1	C
27. Ubon Ratchathani	15.13N 104.51E	12	1	C
29. Nakhon Ratchasima	15.00N 102.06E	177	2	C
30. Lopburi	14.49N 100.37E	6	7	G, C
31. Ang Thong	14.35N 100.25E	14	1	C
34. Suphan Buri	14.14N 100.07E	10	1	C
42. Bangkok	13.39N 100.31E	0	1	G
44. Samut Prakan	13.32N 100.35E	2	1	C
45. Ratchaburi	13.31N 99.47E	19	3	G, C
46. Samut Songkhram	13.25N 100.01E	5	3	G, C
47. Chon Buri	13.21N 100.58E	6	1	O
48. Phetburi	13.05N 99.58E	5	1	C
54. Chantaburi	12.36N 102.07E	6	2	O, C
55. Trat	12.16N 102.30E	12	1	C
56. Prachuap Khiri Khan	11.50N 100.01E	1	6	C

Table I. Continued.

COUNTRY	COORDINATES	ALTITUDE	n	SOURCE
57. Chumphon	10.30N 99.11E	11	3	C
59. Ko Phangan	9.43N 100.00E	16	4	C
60. Ko Samui	9.25N 99.58E	275	6	C
61. Chaiyaphum	9.25N 99.13E	210	1	C
62. Surat Thani	9.07N 99.19E	6	3	G, C
VIETNAM				
1. Sonla	21.19N 103.54E	662	4	G
3. Chieng Khua	20.51N 104.28E	1171	1	G
4. Moc Chau	20.15N 104.37E	1050	1	G
5. Kon Tum	14.22N 107.57E	513	1	G
6. Pleiku	14.07N 108.04E	792	1	G
11. Dalat	11.56N 108.25E	1475	1	G
18. Cho Gao	10.20N 106.28E	0	6	G
19. Pho Quoc Island	10.19N 104.00E	115	2	G
20. Can Tho	10.03N 105.46E	2	1	G
21. Uminh	9.20N 104.54E		4	O, G

* The numbering used in this table is based on the full list of all localities for which *A. florea* has been reported in the literature and is available at http://www.edpsciences.org/apido.

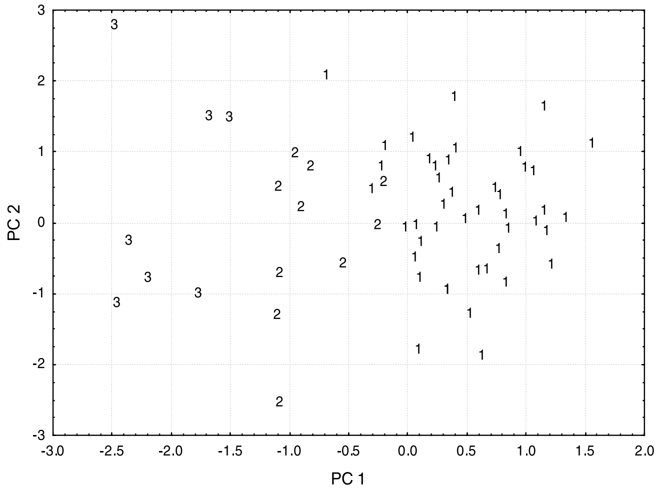

Figure 2. Factor scores (PC) of colony samples of *A. florea* from 1 = Iran, 2 = N. India, 3 = S. India and Sri Lanka.

misclassified two colonies into cluster 2; 90.0% of the colonies (n = 10) from N. India into cluster 2 with a posteriori probabilities P 0.98 for 6 colonies, $0.84 < P < 0.98$ for 3 colonies and misclassified one colony into cluster 1; 100% of the colonies (n = 7) from S. India and Sri Lanka into cluster 3 (smaller bees) with a posteriori probabilities $P = 1.0$ for 5 colonies and $0.97 < P < 1.0$ for 2 colonies. To test the equality of the group means for the characters used in the discriminant function, Wilks' lambda approximated by the F statistic was determined. A significant difference between the means of the three groups was established ($\Lambda = 0.155$, F = 21.2, (8, 110) d.f., $P < 0.0001$).

3.2.5. Vietnam database

In an analysis of the *A. florea* of Vietnam, the databases of Vietnam from Grahamstown and Oberursel were combined (22 colonies). The PC analysis using 9 common characters [(5), (6), (7), (9), (10), (17), B4, D7, G18] isolated two principal components with eigenvalues greater than one: PC 1, size related characters (5), (6), (7), (9), (10), (17) accounted for 50.8% of the variation; PC 2, angles of venation D7 and G18 accounted for 20.7% of the variation. The PC plot revealed a single morphocluster with two indistinct groups: a northern group of larger bees (latitude > 20°) and a southern group of smaller bees (latitude < 10° from Pho Quoc Island and Cho Gao).

3.2.6. Iran, India, Thailand and Vietnam databases

Finally, an analysis was made of the samples from Iran, India, Thailand and Vietnam. Combining the databases of these countries from Bhandari/Sharma, Oberursel and Grahamstown (99 colonies), the PC analysis using 7 common characters [(5), (6), (7), (9), (10), (17), G18] revealed two morphoclusters: a group of larger bees from Iran and another group of bees from India, Thailand and Vietnam along the PC 1 axis and a slight clustering of the colonies from N. India along the PC 2 axis. The first two principal components accounted for 73.7% of the variation in the data: PC 1, size related characters [(5), (6), (7), (9), (10), (17); 56.2%]; PC 2, angle of venation [G18 (25); 17.5%]. Including the Iran data from Tahmasebi (139 colonies) and using 4 common characters [(9+10), (17), G18, LEG], the PC results showed the same two clusters. Including Oberursel's Sri Lanka database (145 colonies) and using 4 common characters [(9+10), (17), G18, LEG], the PC results showed the same two clusters with a slight isolation of smaller bees from S. India and Sri Lanka along the PC 1 axis.

3.3. Multivariate analysis of total morphometric database

Principal components analyses were carried out on the total morphometric databases of Oberursel, Grahamstown, Bhandari/Sharma and Tahmasebi (184 colonies). Using seven morphometric characters of worker honeybees shared in common among the databases [(5), (6), (7), (9), (10), (17), G18] reduced the number of colonies in the analysis to 130. Two principal components with eigenvalues greater than one were isolated: PC 1, size-related characters (5), (6), (7), (9) and (10) with component loadings between 0.85 and 0.90 accounted for 58.9% of the variation; PC 2, angle of venation (25) and size (17) with component loadings 0.87 and 0.57 respectively, accounted for 16.6% of the variation. The two principal components accounted for a total of 75.5% of the variation in the data. The PC plot using the first and second PC scores revealed one morphocluster with an isolation of larger bees from Iran in the far right of the morphocluster along the PC 1 axis and a group of smaller bees from S. India and Sri Lanka in the lower left quadrant. The colonies from Cambodia, India, Myanmar, Nepal, Thailand and Vietnam clustered together along the PC 1 axis. Colonies from Mong La (N. Myanmar), Larkarna (Pakistan) and Seeb (Oman) were closer to the Iran cluster, whilst the colony from Qurm (Oman) was isolated with the smaller bees from S. India and Sri Lanka.

Using these 7 characters in the analysis excluded the Iranian data from Tahmasebi et al. (2002). The analysis was, therefore, repeated using 4 characters common to all databases [(9+10), (17), G18, LEG]. This increased the number of colonies in the analysis to 170 (G18 values were missing in 14 samples) and gave very similar results (Fig. 3). PC 1, size-related

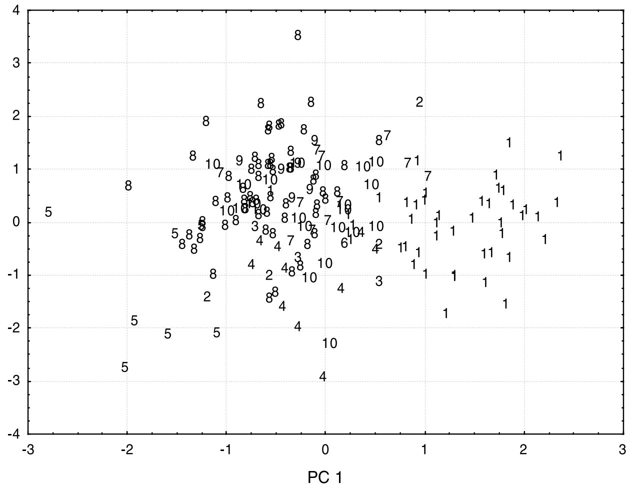

Figure 3. Factor scores (PC) of colony samples of *A. florea* from 1 = Iran, 2 = Oman, 3 = Pakistan, 4 = N. India, 5 = S. India and Sri Lanka, 6 = Nepal, 7 = Myanmar, 8 = Thailand, 9 = Cambodia, 10 = Vietnam.

characters [(9+10), (17) and LEG] with component loadings between 0.88 and 0.92 accounted for 61.4% of the variation; PC 2, angle of venation G18 (25) with component loading 0.98 accounted for 26.4% of the variation. The two principal components accounted for a total of 87.8% of the variation in the data. The morphocluster of larger bees from Iran and the morphocluster of smaller bees from S. India and Sri Lanka are distinct. The discriminant analysis results classified 97.9% of colonies (n = 47) from Iran correctly into group 1 (larger bees) and misclassified one colony into cluster 2; 88.8% of the colonies (n = 116) from N. India, Oman, Pakistan, Cambodia, Myanmar, Thailand, Vietnam into cluster 2 and misclassified five colonies into cluster 1 and eight colonies into cluster 3; 100% of the colonies (n = 7) from S. India and Sri Lanka into cluster 3 (smaller bees).

To test the equality of the group means for the characters used in the discriminant function, Wilks' lambda approximated by the F statistic was determined. A significant difference between the means of the three groups was established ($\Lambda = 0.201$, $F = 50.5$, (8, 328) d.f., $P < 0.0001$).The colony means and standard deviations of nine morphometric characters [(5), (6), (7), (9), (10), (17), G18 (25), (9+10), LEG] averaged for countries are shown in Table II. A cluster analysis using the single linkage (nearest neighbour) procedure was carried out on colony mean character values [(5), (6), (7), (9), (10), (17), G18 (25)] combined for countries (Quinn and Keough, 2002). The results showed a dendrogram of three main clusters (Fig. 4). Phenetically, cluster 1 first linked colonies from Myanmar and Thailand, then Cambodia and finally N. Vietnam; cluster 2 first linked colonies from Oman, N. India and Nepal followed by those from S. India; cluster 3 linked colonies from Iran and Pakistan; colonies from S. Vietnam were linked to clusters 2 and 3.

4. DISCUSSION

4.1. Biogeography

The climatic zones of *A. florea* change from tropical rainforest in the east to savanna at a line between Karachi, New Delhi and Simla in the west. Further westwards, there is a transition from tropical to subtropical steppe and semi-desert. There is a seasonal rainfall gradient across the range of *A. florea* from the eastern tropical to the western subtropical and semi-desert climates of the west (Tab. III). There is also a gradient of mean daily temperature extremes that increases from the eastern tropical zone to the western subtropical zones. In

Table II. Means (m) and standard deviations (sd) of nine morphometric characters (measurements in mm, angles in degrees) of *A. florea* and n = number of colonies.

Character	**Cambodia** n=6	**N. India** n=10	**S. India / Sri Lanka** n=7	**Iran** n=18	**Myanmar** n=11	**Nepal** n=1	**Oman** n=3	**Pakistan** n=3	**Thailand** n=62	**Vietnam** n=22
	m±sd	m±sd	m±sd	m±sd	m±sd	m±sd	m±sd	m±sd	m±sd	m±sd
(5)	1.72±0.02	1.74±0.04	1.67±0.04	1.83±0.03	1.76±0.04	1.74±0.00	1.74±0.06	1.75±0.05	1.74±0.03	1.78±0.02
(6)	2.24±0.03	2.19±0.06	2.09±0.06	2.30±0.03	2.27±0.03	2.29±0.00	2.17±0.08	2.18±0.07	2.22±0.04	2.29±0.03
(7)	1.38±0.02	1.35±0.01	1.29±0.02	1.41±0.03	1.39±0.03	1.39±0.00	1.35±0.04	1.35±0.02	1.35±0.03	1.37±0.01
(9)	1.45±0.03	1.40±0.07	1.32±0.04	1.51±0.04	1.44±0.03	1.47±0.00	1.39±0.05	1.40±0.04	1.41±0.04	1.43±0.02
(10)	1.40±0.02	1.37±0.07	1.27±0.05	1.47±0.04	1.38±0.03	1.40±0.00	1.34±0.04	1.37±0.03	1.36±0.03	1.37±0.02
(17)	6.13±0.05	6.58±0.08	6.14±0.09	6.85±0.13	6.44±0.24	6.33±0.00	6.52±0.18	6.61±0.03	6.17±0.11	6.23±0.06
G18	102.13±1.10	106.20±1.99	106.14±2.89	104.66±1.59	102.71±1.53	105.59±0.00	105.85±0.68	105.10±1.85	102.81±2.16	103.96±1.85
(9+10)	2.85±0.04	2.78±0.12	2.59±0.09	2.96±0.10	2.82±0.06	2.87±0.00	2.73±0.09	2.78±0.07	2.77±0.07	2.80±0.04
LEG	5.34±0.06	5.26±0.11	5.05±0.10	5.54±0.09	5.42±0.11	5.42±0.00	5.26±0.18	5.28±0.14	5.32±0.09	5.44±0.06

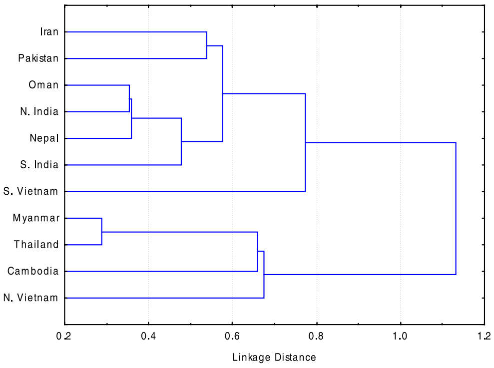

Figure 4. Hierarchical clustering dendrogram for *A. florea*, derived from single linkage clustering on morphometric characters (length of femur (5); length of tibia (6); metatarsus length (7); tergite 3; longitudinal (9); tergite 4; longitudinal (10); forewing length (17); wing angle G18 (25)) averaged for countries.

terms of honeybee movement and dispersal, mean daily temperatures exceed 15° throughout the year in all but China, Nepal, northern areas of India, Pakistan and Iran where temperatures are too low for flight for between 3 and 6 months of the year (Tab. III). The combined rainfall and temperature changes from east to west are reflected in the swarming and migration biology of *A. florea* (Tab. III; cf. Hepburn, 2004). Over this large expanse, reproductive swarming overlaps and occurs at the end of the dry season (March–May). In many areas there is also a second swarming phase before the onset of the drier season of the year (August–October) associated with migration. Therefore, despite climatic and phytogeographical variation, there are no seasonal barriers which would tend to disrupt gene flow within what is actually a panmictic population.

4.2. Morphometric analyses

Radloff and Hepburn (1998, 2000) and Hepburn et al. (2001b) have established empirically that the greater the sampling distances between localities the greater the likelihood that artefactual morphoclusters will emerge in multivariate analyses. Conversely, where between-group variation is larger than within-group variation, biometric subgroups within smaller geographic domains may be swamped and obscured. These principles are particularly useful in analyses of previous studies of *A. florea*.

From a principal components analysis and factor analysis of 20 characters of 18 samples of *A. florea*, Ruttner (1988) obtained three morphoclusters (1) S. India and Sri Lanka, (2) Thailand and (3) Oman, Pakistan and Iran. More recently Tahmasebi et al. (2002) analyzed the *A. florea* of Iran and defined two morphoclusters. Combining their data with that of Ruttner (1988) and Mogga and Ruttner (1988) to form the same groups of countries, they also reported three morphoclusters for *A. florea*. However, in both studies there is a lack of geographical contiguity and each of the three groups is separated from the next by about 3000 km. When we conjointly analyze the whole spectrum of localities sampled, then the clinal nature of the morphometric measurements of this species becomes readily apparent (Fig. 3).

The only comparative, multivariate morphometric study of *A. florea* in Thailand is that of Chaiyawong (2001). The results of her factor and cluster analyses using 22 characters revealed only a single morphocluster. By reducing the number of characters, a degree of isolation from the mainland morphocluster was obtained for Ko Samui and Ko Pha-ngan, but the bees from these localities were correctly regarded simply as variants. The interpretations of Chaiyawong (2001) are confirmed here.

There have been several regional studies of morphometric variation in *A. florea* on a mesoscale level in India and Iran representing sampling intervals of about 3000 km. In northwestern India and Eastern Pakistan, extending along a north-south transect between 25° and 32° N latitude (India localities 1, 4, 7, 11, 25, 31, 43 and Pakistan 53 in Tab. I) a transition in population trends occurs. The general conclusions for this area are that there are significant interlocality differences in the mean values of morphometric characters and their coefficients of variation for most characters measured (Bhandari, 1983; Sharma, 1983; Narayanan et al., 1960), implying heterogeneity in the population. Likewise, *A. florea* of hotter, drier, and lower latitudes are smaller than those at the higher latitudes, leading to the proposition of possibly different ecotypes associated with climate at particular latitudes (Bhandari, 1983; Narayanan et al., 1960), but there are alternative

Table III. Selected climatic data representative of the different regions in which *A. florea* naturally occurs. Rainy months are defined as those in excess of 100 mm/month. Mean daily monthly temperatures suitable for flight are taken at 15 °C. Periods of reproductive swarming and migration are included*.

LOCALITY	RAINS		DRY		TEMP MTHS	SWARM MTHS	MIGRATE MTHS
	MTHS	AMT	MTHS	AMT			
China							
Kunming	5–10	980	11–4	115	4–10	4–5, 9–10	3, 8
Guiyang	5–10	960	11–4	250	4–10	4–5, 9–10	3, 8
Nanning	5–10	1040	11–4	280	3–12	4–5, 9–10	3, 8
Vietnam							
Buon Me Thout	5–10	1560	11–4	230	1–12	7–8	
Hai Phong	5–10	1470	11–4	250	1–12	3–4	
Thailand							
Chiang Mai	5–10	1100	11–4	120	1–12	1–3, 8–10	
Bangkok	5–10	1220	11–4	220	1–12	2–4, 8–10	
Surat Thani	4–12	1700	1–3	110	1–12	4–6, 8–10	
India							
South: Bangalore	5–10	730	11–4	140	1–12	3–4, 10–12	
Central: Nagpur	6–9	1090	10–5	170	1–12		
Northeast: Calcutta	5–10	1455	11–4	145	1–12		
Northwest: New Delhi	7–9	470	10–6	170	2–11		
Northnorth: Simla	6–9	1190	10–5	380	5–9	3–4, 9–10	
Iran							
Northeast: Qandahar	12–3	140	4–11	25	4–10		
Southeast: Chah Bahar	12–2	90	3–11	15	1–12		
Northwest: Esfahan	10–3	70	4–9	10	3–10		
Southwest: Bandar Abbas	12–2	130	3–11	20	1–12	4–5, 7	
Oman							
Ash-Shariqah	12–3	75	4–10	25	1–12	2–4, 9–10	

* Parts of Iran and Oman appear anomalous; however, rainfall never exceeds 100 mm per month in some areas.

views on this point (Sharma, 1983). We obtained a strong significant positive correlation between altitude and the principal components variables reflecting size within the sample from India. This pattern might benefit from additional attention.

Tahmasebi et al. (2002) reported an analysis of *A. florea* from 26 localities in southern Iran extending some 2000 km along an east/west transect between 25° to 35° N latitude (localities 1, 4–6, 8, 10, 13, 14, 16–17, 20–21, 24–25, 27–34, 36–37, and 40–41 in Tab. I). In a principal components analysis of 12 morphometric characters they obtained two morphoclusters in Iran, a western group of larger bees at higher latitudes (29°–34°) and a lower latitude group of smaller bees to the east (< 29° latitude). In our study the PC analysis revealed one morphocluster with two indistinct clusters of smaller eastern and larger western bees.

In studies of variation in mitochondrial DNA, Smith (1991) established that *A. florea* were homogeneous in Thailand and also in southern India but had diverged between the two countries. The homogeneity of mtDNA in *A. florea* from Thailand was subsequently confirmed (Nanork et al., 2001). Smith also observed that different mtDNA clusters occur in *A. cerana* from N. and S. India, paralleling the differences observed in *A. florea.* More recently, Takahashi et al. (unpublished data) proposed three distinct mtDNA lineages for *A. florea* from eastern Asia: (1) China/Myanmar; (2) Southeast Asia: Thailand, Vietnam, Cambodia, and part of China; (3) India. While there are no inconsistencies among these three studies, available information is insufficient to apply to the whole area of *A. florea* distribution. Similarly, available data on enzyme polymorphism in *A. florea* (Li et al., 1986; Sheppard and Berlocher, 1989; Gan et al., 1991) are likewise geographically limited precluding extrapolation to the whole *A. florea* population. The available genetic data are too regional in nature to be informative for the species as a whole.

4.3. Classification

Much of the apicultural and geographical literature of the 19th century was exploratory and descriptive in nature. Specimens exhibiting small differences from previously collected specimens were named, elevating them to taxonomic status. However, the history of the classification of infraspecific categories of *A. florea* contrasts with that of other Asian species of honeybees in several interesting ways. Maa (1953) was an eminent museum taxonomist whose work has almost universally been regarded as belonging to the "splitters school", particularly with regard to the many taxa erected for *A. cerana* and *A. mellifera*. Yet, Maa (1953) synonymized all previous infraspecific taxa of *A. florea* and *A. andreniformis,* a view that still prevails (Engel, 1999). The apparent lack of infraspecific taxa in the two dwarf honeybee (*Micrapis*) species may reflect a limited dispersal ability, as evidenced by their absence on most offshore island groups (Otis, 1997). This apparent inability of *A. florea* to disperse from peripheral populations, coupled with synchronous reproductive seasons across its distribution, have apparently limited regional differentiation of these species into recognizable subspecies/races.

The comparisons of *A. florea* from India/Sri Lanka (3.2.2 above) or Iran, India, Thailand and Vietnam (3.2.6 above) both yielded two morphoclusters. Similarly, the analyses of Ruttner (1988) and Tahmasebi et al. (2002) yielded three morphoclusters and precisely the same result is shown in Figures 2 and 3. As previously noted, the effects of sample size and interlocality distance have major implications for morphocluster group formation (Radloff and Hepburn, 1998). Here, the distributional variation in morphometric characters is clinal: northwestern bees are larger than southeastern ones. In the final analysis, *A. florea* is a single species comprised of three discernible morphoclusters. The northwestern-most bees comprise a morphocluster (1) that is statistically quite distinct from that to the southeast (3); but, they are not isolated, they are joined by large areas of intermediate forms (2) resulting in a continuous cline in morphometric traits within this panmictic species.

ACKNOWLEDGEMENTS

We are grateful to Hu Fuliang, Hangzhou, China, for arranging translations of the Chinese. We thank N. Tajabadi, M. Akhoundi and S. Faraji for providing relevant data from Iran and Amssalu B. for technical assistance.

Résumé – **Analyse morphométrique multivariée d'*Apis florea*.** Différentes sous-espèces et variétés d'*Apis florea* Fabricius 1787 ont été décrites au cours des deux siècles passés. Elles ont été ensuite regroupées par Maa (1953). Depuis, quelques études régionales ont été menées mais elles n'ont pas en fait influencé la classification. Dans le présent travail ont été rassemblées les données provenant de plusieurs banques de données (Oberursel, Grahamstown) et des recherches de Bhandari (1983), Sharma (1983), Tahmasebi et al. (2002) et Chaiyawong (2001) et de nouvelles données ont été ajoutées. On a pu ainsi faire une analyse multivariée portant sur 2923 ouvrières prélevées dans 184 colonies réparties dans 103 lieux dispersés dans toute la zone de répartition d'*A. florea* (Fig. 1).

Il ressort en premier lieu qu'*A. florea* se différencie sans équivoque d'*A. andreniformis* par la morphologie. La comparaison des populations séparées géographiquement fournit tout d'abord des groupes morphologiques (morphoclusters) (Fig. 2). Mais ceux-ci reflètent des artéfacts liés à l'échantillonnage et disparaissent dès que l'ensemble des données est inclus dans une même analyse en composantes principales. Malgré cela une analyse de groupement (cluster analysis) sur la base des distances euclidiennes montre des affinités entre groupements géographiquement voisins. Il en résulte que l'*A. florea* présente un seul groupe morphologique sans sous-regroupements nets. Les caractères morphométriques varient selon un gradient géographique, ou cline, en fonction de la latitude et l'altitude. La variation n'est pas suffisante au sein des données et de l'analyse pour identifier des taxons infraspécifiques. L'espèce a une aire de répartition très étendue, depuis les forêts pluviales jusqu'aux steppes subtropicales en passant par les zones de savanes. L'essaimage reproductif a lieu de façon continue dans le temps permettant un flux de gènes au sein de cette espèce panmictique.

***Apis florea* / morphométrie / répartition géographique / biogéographie / essaimage / migration**

Zusammenfassung – Multivariate morphometrische Analyse von *Apis florea.* In den letzten 2 Jahrhunderten wurden verschiedene Unterarten und Varietäten von *Apis florea* Fabricius 1787 beschrieben, diese wurden später von Maa (1953) wieder zusammengefasst. Seither wurde einige Untersuchungen über mittelgrosse Areale durchgeführt, die die Klassifikation allerdings nicht beeinflussten. In der vorliegenden Untersuchung wurden die Daten aus mehreren Datenbanken (Oberursel, Grahamstown) und Untersuchungen Bhandari (1983), Sharma (1983), Tahmasebi et al. (2002) und Chaiyawong (2001) zusammengeführt und durch neue Daten ergänzt. Hierdurch konnte eine multivariate Analyse über 2923 Arbeiterinnen aus 184 Völkern von 103 über das gesamte Verbreitungsgebiet von *A. florea* verteilten Fundorten durchgeführt werden (Abb. 1).

Zunächst zeigte sich, dass *A. florea* morphologisch eindeutig von *A. andreniformis* abgegrenzt werden kann. Der Vergleich von durch größere geographische Distanzen getrennten Datensätzen ergaben zunächst Morphokluster (Abb. 2). Diese sind allerdings auf die Begrenztheit der Sammlung zurückzuführen und verschwinden, sobald die gesamte Datenmenge in die Hauptkomponentenanalyse eingeschlossen wird. Dessen ungeachtet zeigt eine Klusteranalyse auf Basis der euklidischen Distanzen Affinitäten zwischen geographisch benachbarten Gruppierungen auf. Im Resultat ergibt sich aus der Analyse, dass *A. florea* einen einzigen Morphokluster ohne deutliche Untergruppierungen aufweist, dieser ist allerdings klinal entlang der geographischen Länge und Meereshöhe strukturiert. Innerhalb der Einschränkungen des Datenmaterials und der Analyse reicht die gegebene Variationsbreite nicht aus, um infraspezifische Taxa zu identifizieren. Die Spezies hat ein sehr ausgedehntes Verbreitungsgebiet, geographisch umfasst dieses Gebiete mit tropischen Regenfällen über Savannengebiete bis zur subtropischen Steppe. Allerdings ist die Saisonalität des reproduktiven Schwärmens derart, dass sich über die gesamte Population ein zeitlicher Zusammenhang ergibt (Tab. III).

***Apis florea* / Morphometrie / Verbreitung / Biogeographie / Schwarm / Wanderung**

REFERENCES

Aggarwal K., Kapil R.P. (1988) Seasonal population dynamics of *Tropilaelaps clareae* (Acari: Laelapidae) in *Apis dorsata* colonies, in: Channabasavanna G.P., Viraktamath C.A. (Eds.), Progress in Acarology, Oxford and IBH Publishing Company, New Delhi, India, pp. 283–286.

Akratanakul P. (1977) The natural history of the dwarf honey bee, *Apis florea* F. in Thailand, Thesis, Cornell University, Ithaca, New York, pp. 1–91.

Bhandari V.C. (1983) Biometrical studies on *Apis florea* F. and *Apis dorsata* F. of north-western India, Thesis, Himachal Pradesh University, Simla, India, pp. 1–92.

Chaiyawong T. (2001) Morphometric study of *Apis florea* in Thailand, MSc. Thesis, Chulalongkorn University, Bangkok, Thailand, 108 p.

Chen Y. (1993) Apiculture in China, Agricultural Scitech Publishing House of China, Beijing, pp. 1–178.

Cockerell T.D.A. (1911) Descriptions and records of bees XXXV, Ann. Mag. Nat. Hist. Series London 8, 310–319.

Deodikar G.B., Ghatge A.L., Phadke R.P., Mahindre D.B., Kshirsagar K.K., Muvel K.S., Thakar C.V. (1977) Nesting behaviour of Indian honeybees. III. Nesting behaviour of *Apis dorsata* Fab., Indian Bee J. 39, 1–12.

Dover C. (1929) Wasps and bees in the Raffles Museum, Singapore, Bull. Raffles' Museum Singapore 2, 43–70.

Drory E. (1888) From my notebook: notes on bees from a trip around the world, Bienenvater 20, 20–30 (in German).

Dung P.X., Thai P.H., Trung L.Q. (1996) Some comparative characteristics between *Apis florea* and *Apis andreniformis* in Minh Hai Province, Proc. 3rd Asian Apic. Assoc. Hanoi, p. 62.

Dutton R.W., Free J.B. (1979) The present status of beekeeping in Oman, Bee World 60, 176–185.

Enderlein G. (1906) New honeybees and contribution to the distribution of the genus *Apis*, Stett. Entomol. Ztg. 67, 331–334 (in German).

Engel M.S. (1999) The taxonomy of recent and fossil honey bees (Hymenoptera: Apidae; *Apis*), J. Hymenoptera Res. 8, 165–196.

Fabricius J.C. (1787) Mantissa Insectorum, Hafniae, Proft. Vol. 1, p. 348 (cited from Maa, 1953).

Free J.B. (1981) Biology and behaviour of the honeybee, *Apis florea*, and possibilities for beekeeping, Bee World 62, 46–59.

Gan Y.Y., Otis G.W., Mardan M.B., Tan S.G. (1991) Allozyme diversity in Asian *Apis*, in: Smith D.R. (Ed.), Diversity in the Genus *Apis*, Westview Press, Boulder, Co., pp. 117–130.

Gerstäcker C.E.A. (1863) On the geographical distribution of honeybees, Ann. Mag. Nat. Hist. London 11, 270–283; 333–347.

Ghatge A. (1949) Some research work on *Apis florea*, Indian Bee J. 11, 5–6; 9.

Hepburn H.R. (2004) Absconding, migration and swarming in honeybees: an ecological and evolutionary perspective, Proc. IUSSI Conference on Social Insects, St. Petersburg (in press).

Hepburn H.R., Hepburn C. (2005) Bibliography of *Apis florea*, Apidologie, 36, 377–378 (available at http://www.edpsciences.org/apido).

Hepburn H.R., Smith D.R., Radloff S.E., Otis G.W. (2001a) Infraspecific categories of *Apis cerana*: morphometric, allozymal and mtDNA diversity, Apidologie 32, 3–23.

Hepburn H.R., Radloff S.E., Verma S., Verma L.R. (2001b) Morphometric analysis of *Apis cerana* populations in the southern Himalayan region, Apidologie 32, 435–447.

Johnson R.A., Wichern D.W. (1998) Applied Multivariate Statistical Analysis, 4th ed., Prentice Hall, Upper Saddle River, New Jersey.

Koeniger G. (1991) Diversity in *Apis* mating systems, in: Smith D.R. (Ed.), Diversity in the Genus *Apis*, Westview Press, Boulder, Co., pp. 199–212.

Koeniger N., Koeniger G. (1991) An evolutionary approach to mating behaviour and drone copulatory organs in *Apis*, Apidologie 22, 581–590.

Koeniger N., Koeniger G. (2000) Reproductive isolation among species of the genus *Apis*, Apidologie 31, 313–339.

Koeniger N., Koeniger G. (2001) Behavioural mating barriers among sympatric species of the genus, *Apis*, Proc. 7th Int. Conf. Apic. Trop. Climates, Chiang Mai, pp. 80–85.

Kuang B.Y., Li Y.C. (1985) The genus *Apis* in China, Chinese Beekeeping 76, 7–9 (in Chinese).

Lavrekhin F.A. (1935) Contribution to the study of variation of the honey bee. 2. A comparative biometric characteristic of the sexual appendages of the drones belonging to different forms of the genus *Apis*, Zool. Zh. 14, 655–663 (in Russian).

Li S., Meng Y.P., Chang J.T., Li J.H., He S.Y., Kuang B.Y. (1986) A comparative study of esterase isozymes in 6 species of *Apis* and 9 genera of Apoidea, J. Apic. Res. 25, 129–133.

Maa T. (1953) An enquiry into the systematics of the tribus *Apidini* or honey bees (Hymenoptera), Treubia 21, 525–640.

Mehta V.K. (1948) *Apis florea*, Indian Bee J. 10, 79–81.

Millen T.W. (1944) *Apis florea*, Indian Bee J. 6, 106–108.

Mogga J., Ruttner F. (1988) *Apis florea* in Africa: source of the founder population, Bee World 69, 100–103.

Mossadegh M.S. (1991) Geographical distribution, levels of infestation and population density of the mite *Euvarroa sinhai* Delfinado and Baker (Acarina: Mesostigmata) in *Apis florea* F. colonies in Iran, Apidologie 22, 127–134.

Müller M.J. (1982) Selected Climatic Data for a Global Set of Standard Stations for Vegetation Sciences, Junk, The Hague.

Muttoo R.N. (1957) Some so called "peculiarities" of behaviour of Indian honeybees as compared to the European bees, Indian Bee J. 19, 62–64.

Nanork P., Deowanish S., Wongsiri S. (2001) Mitochondrial DNA variability of dwarf honey bee [*Apis florea* Fabricius (1787)] in Thailand by using PCR-RFLP technique, Proc. 7th Int. Conf. Apic. Trop. Climates, Chiang Mai, pp. 341–345.

Narayanan E.S., Sharma P.L., Phadke K.G. (1960) Studies on biometry of the Indian bees II. Tongue length, wing hooks, worker-brood-cell size and thickness of comb of *Apis florea* F. at Pusa (Bihar), Indian Bee J. 22, 81–88.

Nunamaker R.A., Wilson W.T., Ahmad R. (1984) Malate dehydrogenase and non-specific esterase isoenzymes of *Apis florea*, *A. dorsata*, and *A. cerana* as detected by isoelectric focusing, J. Kansas Entomol. Soc. 57, 591–595.

Otis G.W. (1991) A review of the diversity of species within *Apis,* in: Smith D.R. (Ed.), Diversity in the Genus *Apis*, Westview Press, Boulder, Colorado, pp. 29–49.

Otis G.W. (1997) Distributions of recently recognized species of honey bees (Hymenoptera: Apidae; *Apis*) in Asia, J. Kansas Entomol. Soc. 69 (Suppl.), 311–333.

Quinn G.P., Keough M.J. (2002) Experimental Design and Data Analysis for Biologists, Cambridge University Press, Cambridge.

Radloff S.E., Hepburn H.R. (1998) The matter of sampling distance and confidence levels in the subspecific classification of honeybees, *Apis mellifera* L., Apidologie 29, 491–501.

Radloff S.E., Hepburn H.R. (2000) Population structure and morphometric variance in the *Apis mellifera scutellata* group of honeybees in Africa, Genet. Mol. Biol. 23, 305–316.

Rao P.V. (1998) Statistical Research Methods in Life Sciences, Brooks/Cole Publishing Company, Pacific Grove, CA.

Rinderer T.E., Oldroyd B.P., Wongsiri S., Sylvester H.A., De Guzman L.I., Potichot S., Sheppard W.S., Buchmann S.L. (1993) Time of drone flight in four honey bee species in south-eastern Thailand, J. Apic. Res. 32, 27–33.

Rinderer T.E., Oldroyd B.P., Wongsiri S., Sylvester H.A., De Guzman L.I., Stelzer J.A., Riggio R.M. (1995) A morphological comparison of the dwarf honey bees of south-eastern Thailand and Palawan, Philippines, Apidologie 26, 387–394.

Rinderer T.E., Wongsiri S., Kuang B.Y., Liu J.S., Oldroyd B.P., Sylvester H.A., De Guzman L.I. (1996) Comparative nest architecture of the dwarf honey bees, J. Apic. Res. 35, 19–26.

Ruttner F. (1975) A metatarsal clasping structure in the *Apis* drone, Entomol. Ger. 2, 22–29.

Ruttner F. (1988) Biogeography and Taxonomy of Honeybees, Springer-Verlag, Berlin, Germany, pp. 1–284.

Ruttner F. (1992) Naturgeschichte der Honigbienen, Ehrenwirth, Munchen, Germany.

Sharma P.C. (1983) Morphometric studies on *Apis florea* F. and *Apis dorsata* F. of Himachal Pradesh and Punjab, Thesis, Himachal Pradesh University, India, pp. 1–83.

Sheppard W.S., Berlocher S.H. (1989) Allozyme variation and differentiation among four *Apis* species, Apidologie 20, 419–431.

Sihag R.C., Abrol D.P. (1986) Correlation and path-coefficient analysis of environmental factors influencing flight activity of *Apis florea* F., J. Apic. Res. 25, 202–208.

Smith D.R. (1991) Mitochondrial DNA and Honey Bee Biogeography, in: Smith D.R. (Ed.), Divserity in the Genus *Apis*, Westview Press, Boulder, Co., pp. 131–176.

Smith F. (1858) Catalogue of the hymenopterous insects collected at Sarawak, Borneo, Proc. Linn. Soc. London 2, 42–130.

Soman A.G., Chawda S.S. (1996) A contribution to the biology and behaviour of the dwarf bee, *Apis florea* F. and its economic importance in Kutch, Gujarat, India, Indian Bee J. 58, 81–88.

Tahmasebi G., Ebadi R., Tajabadi N., Akhoundi M., Faraji S. (2002) The effects of geographical and climatic conditions on the morphological variation and seperation of Iranian small honeybee (*Apis florea* F.) populations, J. Sci. Technol. Agric. Nat. Res., Iran 6, 169–176.

Thakar C.V., Tonapi K.V. (1962) Nesting behaviour of Indian honeybees. II. Nesting habits and comb cell differentiation in *Apis florea* Fab., Indian Bee J. 24, 27–31.

Tirgari S. (1971) On the biology and manipulation of *Apis* (*Micrapis*) *florea* F. in Iran, Proc. 23rd Int. Beek. Congr., pp. 330–332.

Troll C., Paffen K.H. (1980) Jahreszeitenclimate der Erde, Berlin.

Verma L.R., Kafle G.P., Sharma A., Mattu V.K. (1989) Biometry of *Apis cerana* of Nepal Himalayas, in: Proc. 4th Int. Conf. Apic. Trop. Climates, pp. 458–465.

Verma L.R., Mattu V.K., Daly H.V. (1994) Multivariate morphometrics of the Indian honeybee in the northwest Himalayan region, Apidologie 25, 203–223.

von Buttel-Reepen H. (1906) Contributions to the systematics, biology as well as the historical and geographical distribution of honeybees (*Apis mellifica* L.) their variability and other *Apis* species, Mitt. Zool. Museum Berlin 3, 117–201 (in German).

Wongsiri S., Limbipichai K., Tangkanasing P., Mardan M., Rinderer T., Sylvester H.A., Koeniger G., 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.

Wu Y.R., Kuang B. (1986) A study of the genus *Micrapis* (Apidae), Zool. Res. 7, 99–102 (in Chinese).

Wu Y.R., Kuang B. (1987) Two species of small honeybee – a study of the genus *Micrapis*, Bee World 68, 153–155.