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Original article

Population structure and classification of *Apis cerana**

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Abstract – Multivariate morphometric analyses of *Apis cerana* Fabricius, 1793 across its full geographical range were performed. Principal components plots did not reveal distinct morphoclusters. Further substructuring of the principal component plots could not initially be derived but only by introducing local labelling did it reveal six main morphoclusters. We apply geographically based common epithets to the morphoclusters and designate them as: as "Northern *cerana*", "Himalayan *cerana*" "Indian plains *cerana*" "Indochinese *cerana*" "Philippine *cerana*" and "Indo-Malayan *cerana*". *A. cerana* naturally occurs in climatic zones ranging from rainforest, savanna, steppe, grasslands and deciduous forest to taiga. The distributions of the morphoclusters are related to these physiographic and climatic factors. The taxonomy of *A. cerana* is formally revised and synonymous specific and infraspecific names summarized.

***Apis cerana* / subspecies / morphometrics / biogeography**

1. INTRODUCTION

Unraveling the structural complexity of *Apis cerana* (Fabricius, 1793) has been a historically continuous process. Having largely abandoned the typological approach of Maa (1953) and adopted the multivariate techniques of DuPraw (1964, 1965), Ruttner (1988) published the first comprehensive, multivariate statistical analyses of *A. cerana*, which proved seminal in stimulating further research. Subsequent authors used Ruttner's interpretations of *A. cerana* as a new baseline and concentrated on morphoclusters derived from multivariate analyses on a microscale level (Muzaffar and Ahmad, 1989; Pesenko et al., 1989; Rinderer et al., 1989; Limbipichai, 1990; Otis and Hadisoesilo, 1990; Singh et al., 1990; Sulistianto, 1990; Szabo, 1990; Verma, 1990, 1992; Verma et al., 1989, 1994; Kwon and Huh, 1992; Ono, 1992; Damus, 1995; Hadisoesilo et al., 1995; Fuchs et al., 1996; Sylvester et al., 1998) as well as a more regional, mesoscale level (Peng et al., 1989; Yang, 1986, 2001; Diniz-Filho et al., 1993; Damus, 1995; Damus and Otis, 1997; Hepburn et al., 2001b; Tilde et al., 2000; Kuang

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et al., 2002; Radloff and Hepburn, 2002; Tan et al., 2002; Radloff et al., 2003, 2005a, b, c). Hepburn and Radloff (1996, 1998) designated statistically defined populations of honey bees under the new coinage of "morphoclusters". This obviated the use of infraspecific names previously applied to the *A. cerana* group (Hepburn et al., 2001a), because the typological approach is fundamentally incompatible with a statistical one.

Here we report the results of a multivariate morphometric analysis of *A. cerana* across its full geographical range and identify the statistically defined morphoclusters and subcluster populations within them. We consider the relationships of morphoclusters to each other, their geophysical and ecological surroundings and present a new distribution map for *A. cerana* based on 2687 references (Hepburn and Hepburn, 2006). Comments on gene flow or degree of temporal reproductive isolation are suggested from swarming and migration data. Finally, we apply geographically based common names to the morphoclusters and subclusters as is the general practice in economic entomology and ornithology.

2. MATERIALS AND METHODS

2.1. Honey bees

The worker honey bee specimens, used for the combined mainland and oceanic *A. cerana* analysis, derive from several different sources: (1) new material was collected in Japan, Korea and Russia (25 colonies); (2) raw databases of the Institut für Bienenkunde at Oberursel (Germany), Grahamstown (South Africa), Bogor (Indonesia) and Kunming (China); (3) raw databases of previously published results for India and Nepal (Singh et al., 1990; Singh and Verma, 1993; Verma et al., 1989, 1994; Hepburn et al., 2001b), for Afghanistan and Pakistan (Radloff et al., 2005a), for Philippines and Indonesia (Rinderer et al., 1989; Sulistianto, 1999; Tilde et al., 2000) (n = 964 colonies; Tab. 1, supplementary material). Previous classification results of processed data for Japan from Akahira and Sakagami (1959a, b) and for Sri Lanka from Szabo (1990) and additional information based on statistically processed data for Thailand, Indonesia and Malaysia from Limbipichai (1990); Damus (1995); Damus and Otis (1997) and for Thailand from Sylvester et al. (1998) were incorporated into the final population structure and classification of *A. cerana* table (Radloff et al., 2005c). The geographical origins of *A. cerana* worker honey bees from 1067 colonies at 354 localities are listed in Table 1 (supplementary material) and shown in Figure 1.

2.2. Measurements

Twelve morphological characters of worker honey bees common to the Ruttner/Oberursel, Kunming and Grahamstown databases as well as those in the present study were utilized (n = 964 colonies). Their Ruttner (1988) and Verma et al. (1989, 1994) character numbers are given in round and square brackets, respectively, as follows: length of metafemur (5) [30], length of metatibia (6) [31], metatarsus length (7) [32], tergum 3, longitudinal (9) [42], tergum 4, longitudinal (10) [45], sternum 3, longitudinal (11) [49], wax plate of sternum 3, longitudinal (12) [48], sternum 6, longitudinal (15) [50], forewing length (17) [5], wing angle B4 (22) [10], wing angle D7 (23) [11] and wing angle G18 (25) [13].

2.3. Data analysis

Multivariate statistical analysis of the data (using 12 morphometric characters) included principal components analysis to identify possible morphoclusters and subclusters for *A. cerana*, hierarchical cluster analysis to identify homogeneous morphoclusters, linear discriminant analysis to determine the percentages of correct classification of colonies in each morphocluster, Wilks' lambda statistic for testing significant differences between the multiple means of the characters entered into the discriminant functions and Levene's F statistic procedure for testing heterogeneity of variances (Johnson and Wichern, 2002). All statistical analyses were performed using Statistica (StatSoft, 2007).

2.4. Definitions

The sympatric occurrence of *A. cerana* with other medium-sized bees, *A. koschevnikovi, A. nigrocincta* and *A. nuluensis* in Southeastern Asia unfortunately means that an undeterminable amount of some previous "*A. cerana*" literature may inadvertently include data derived from species other

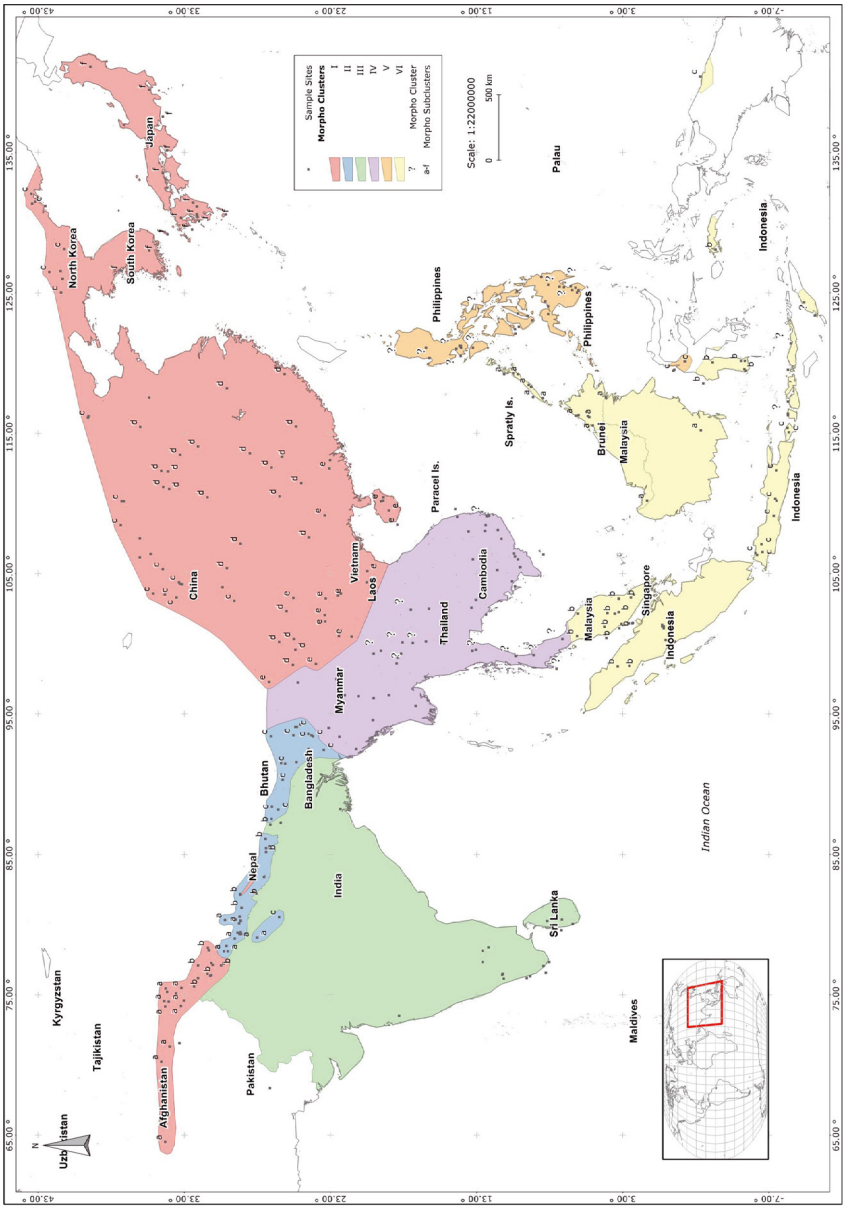

Figure 1. Geographical distribution of the six *Apis cerana* morphocluster groups and identifiable subspecific populations obtained in the current analysis.

than *A. cerana* (Hepburn et al., 2001a). To assist in overcoming this problem, we list metric characters that in combination separate these four species of *Apis* even if they are pinned museum specimens as follows. The cubital index of the forewings are *A. cerana* = 3.9, *A. koschevnikovi* = 7.2, *A. nigrocincta* = 3.7, and *A. nuluensis* = 2.4, which quickly separates paired comparisons for all but an *A. cerana* and *A. nigrocincta* option. To further separate *A. cerana* from *A. nigrocincta*, the length of the basal portion of the radial cell of the forewing is 1.2 mm in *A. cerana*, 1.8 mm in *A. nigrocincta*; length of the apical portion of the radial cell is 1.8 mm in *A. cerana*, 1.1 mm in *A. nigrocincta*; the length of the labial palp is 1.8 mm in *A. cerana*, 3.7 mm in *A. nigrocincta*.

3. RESULTS

3.1. Morphoclusters

Principal components analysis using twelve morphometric characters of worker honey bees ((5), (6), (7), (9), (10), (11), (12), (15), (17), B4, D7, G18) was carried out on the morphometric mainland and oceanic databases of Oberursel, Kunming, Bogor, Grahamstown, Rinderer et al. (1989), Sulistianto (1990), and Tilde et al. (2000) comprising 964 colonies. Three principal components with eigenvalues greater than one were isolated. PC 1: size-related characters (5), (6), (7), (9), (10), (11), (12), (15) and (17) with component loadings between 0.76 and 0.95 accounted for 63.1% of the variation; PC 2: angles of venation (22) and (23) with component loadings 0.66 and 0.75, respectively, accounted for 10.4% of the variation; PC 3: angle of venation (25) with component loading 0.91 accounted for 8.4% of the variation. The three principal components accounted for a total of 81.9% of the variation in the data.

PC plots using both the first and second PC scores and the first and third PC scores did not reveal distinct morphoclusters. Further substructuring of the PC plots by introducing local labelling and running a hierarchical cluster analysis using the mean scores for PC 1 to 3 to identify homogeneous morphoclusters revealed six main overlapping morphoclusters and are defined as follows (Fig. 2):

(1) Morphocluster I, here named "Northern *cerana*", extends from northern Afghanistan and Pakistan through northwest India, across southern Tibet, northern Myanmar, China and then northeasterly into Korea, far eastern Russia and Japan (Fig. 2). Six subclusters or populations are morphometrically discernible within this morphocluster: (a) an "Indus" group in Afghanistan, Pakistan and Kashmir; (b) a "Himachali" group in Himachal Pradesh, India; (c) an "Aba" group in southern Ganshu and central and northern Sichuan provinces in China, northern China and Russia (larger bees); (d) a subcluster in central and eastern China; (e) a "southern" *cerana* subcluster in southern Yunnan, Guangdong, Guangxi and Hainan in China; and (f) a "Japonica" group in Japan and Korea (Fig. 1). Morphocluster I bees have been previously named as follows: *A. skorikovi*, *A. c. abansis*, *A. c. abanensis*, *A. c. bijjieca*, *A. c. cathayca*, *A. c. cerana*, *A. c. fantsun*, *A. c. hainana*, *A. c. hainanensis*, *A. c. heimifeng*, *A. c. indica*, *A. c. japonica*, *A. c. javana*, *A. c. kweiyanga*, *A. c. maerkang*, *A. c. pekinga*, *A. c. peroni*, *A. c. skorikovi*, *A. c. shankianga* and *A. c. twolareca.*

(2) Morphocluster II, here named "Himalayan *cerana*" includes the bees of northern India: (a) northwest, (c) northeast; and some of southern (c) Tibet and Nepal. Two subclusters are discernible within this morphocluster, which we term the bees of the northwest the "Hills" group, and those of the northeast, the "Ganges" group (Figs. 1 and 2). Morphocluster II bees have previously been named *A. c. skorikovi*, *A. c. indica*, *A. c. himalayana*, and *A. c. himalaya*.

(3) Morphocluster III, here named "Indian Plains *cerana*" occurs across the plains of central and southern India and Sri Lanka as a fairly uniform population, long known as "plains *cerana*" for this subcontinent (Figs. 1 and 2). Morphocluster III bees have only previously been termed *A. c. indica*.

(4) Morphocluster IV, here named "Indochinese *cerana*" form a compact group in Myanmar, northern Thailand, Laos, Cambodia and more southern Vietnam (Figs. 1 and 2).

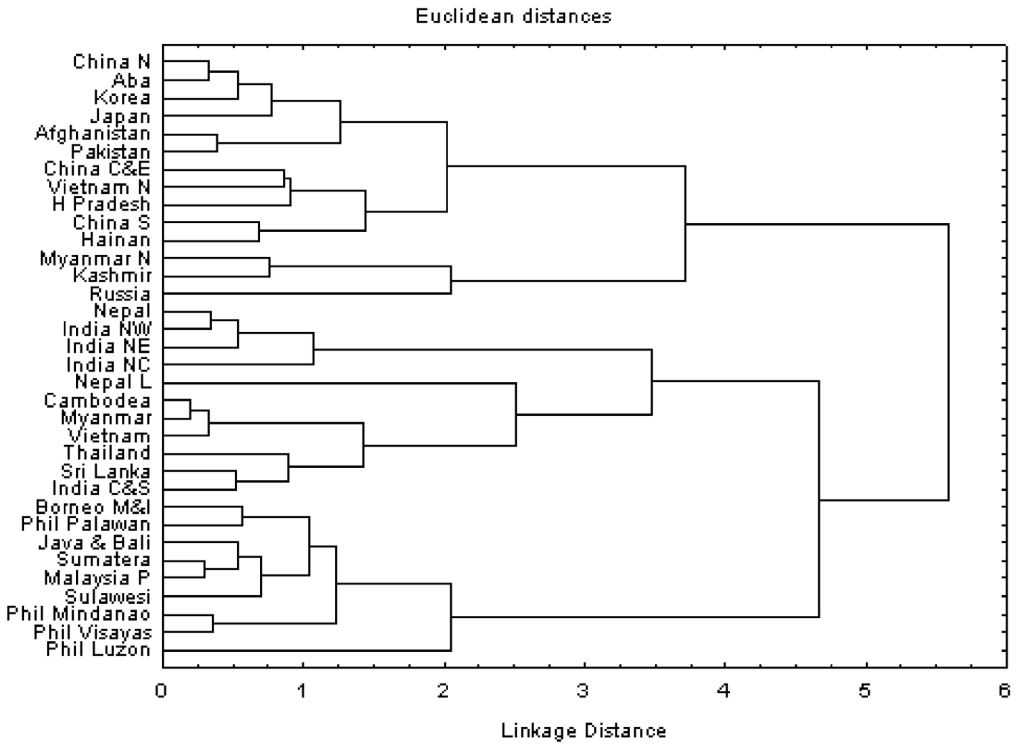

Figure 2. Hierarchical clustering dendrogram for *A. cerana*, derived from complete linkage clustering on 12 morphometric characters (Ruttner numbers, (5), (6), (7), (9), (10), (11), (12), (15), (17), B4 (22), D7 (23) and G18 (25)) averaged for regional groups and countries.

Morphocluster IV bees have been previously named *A. c. indica* and *A. c. javana.*

(5) Morphocluster V, here named "Philippine *cerana*" is restricted to the Philippines, but excluding most of Palawan Island which group with Morphocluster VI. Within these islands there are subclusters and we term these bees respectively after the major island groups there: "Luzon" bees, "Mindanao" bees, and "Visayas" bees. The latter two subclusters showed closer morphometric similarity than the former (Figs. 1 and 2). Morphocluster V bees have been previously named *A. philippina*, *A. c. philippina* and *A. c. samarensis*.

(6) Morphocluster VI, here named "Indo-Malayan cerana", extend from southern Thailand, through Malaysia and Indonesia. This large area consists of a morphometrically rather uniform bee below the South China Sea. Three subclusters are discernible within this morphocluster: (a) Philippines (Palawan), Malaysia (North Borneo), Indonesia (Kalimantan) bees; (b) Malay Peninsula, Sumatera, and some Sulawesi bees; (c) Indonesia (Java, Bali, Irian Jaya, some Sulawesi and Sumatera) bees (Figs. 1 and 2). Morphocluster VI bees have been previously termed *A. cerana*, *A. indica, A. javana, A. c. johni*, *A. lieftincki*, *A. peroni*, *A. vechti linda* and *A. v. vechti*.

The results of a linear discriminant analysis using 12 morphometric characters classified: 95.3% of colonies (n = 342) from Morphocluster I correctly and misclassified 17 colonies; 94.5% of colonies (n = 155) from Morphocluster II correctly and misclassified 9 colonies; 95.1% of colonies (n = 77) from Morphocluster III correctly and misclassified 4 colonies; 95.3% of colonies (n = 121) from

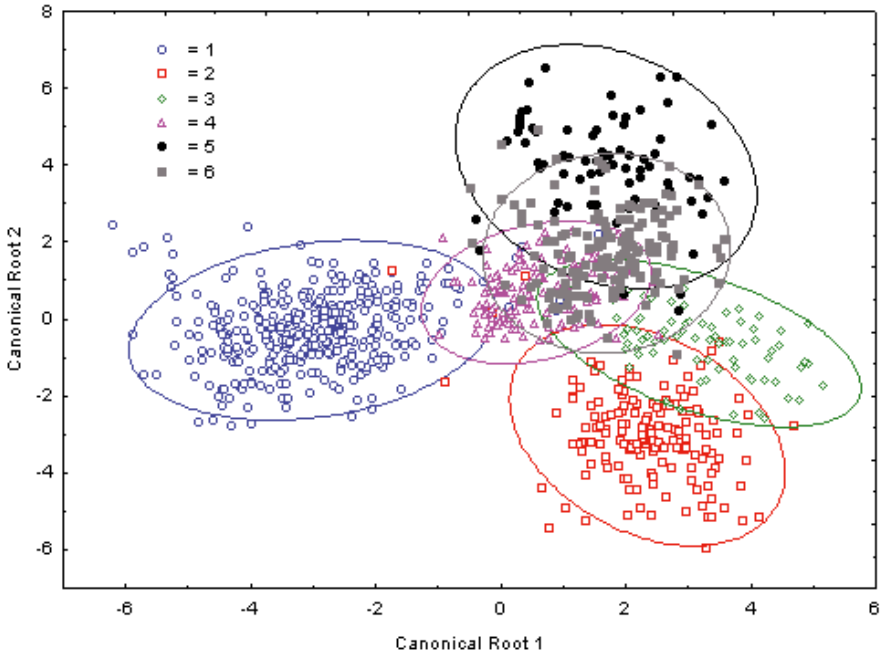

Figure 3. Discriminant analysis plot of six morphoclusters of *A. cerana* using colony means of 12 common morphometric characters. Numbers indicate colonies from morphoclusters: 1 = colonies from northern Afghanistan, Pakistan, Kashmir, Himachal Pradesh, northern Myanmar and northern Vietnam, China, Russia, Japan and Korea; 2 = colonies from northwestern and northeastern India, some of southern Tibet and Nepal; 3 = colonies from central and southern India and Sri Lanka; 4 = colonies from Myanmar, Thailand, Cambodia and central and southern Vietnam; 5 = colonies from Philippines (Luzon, Mindanao and Visayas); 6 = colonies from Philippines (Palawan), Malaysia and Indonesia.

Morphocluster IV correctly and misclassified 6 colonies; 89.5% of colonies (n = 68) from Morphocluster V correctly and misclassified 8 colonies; and 80.4% of colonies (n = 123) from Morphocluster VI correctly and misclassified 30 colonies. Overall 92.3% of the colonies were correctly classified into the morphclusters. A significant difference between the means of the six morphoclusters was established (Wilks' test: Λ = 0.0089, $F_{60,4428}$ = 128.4, P < 0.0001). Canonical 1 and 2 scores plot showed the morphoclusters are not disjoint (Fig. 3, confidence ellipses at 95%).

3.2. Taxonomy of *A. cerana*

The ICZN summary of the taxonomy for *A. cerana* is summarized here, with the formal synonymy of subspecific and other names noted as required nomenclaturally:

***Apis cerana* Fabricius**

Apis cerana Fabricius, 1793: 327.
Apis indica Fabricius, 1798: 274.
Apis socialis Latreille, 1804a: 390.
Apis peroni Latreille, 1804b: 173.
Apis gronovii Guillou, 1841: 323.
Apis perrottetii Guérin-Méneville, 1844: 461.
Apis delessertii Guérin-Méneville, 1844: 461.
Apis sinensis Smith, 1865: 380.
Apis mellifica variety *japonica* Radoszkowski, 1887: 436.
Apis delesserti Buttel-Reepen, 1906: 168. *Nomen vanum* (unjustified emendation) [ICZN Article 33.2.3].
Apis indica variety *javana* Enderlein, 1906: 337.
Apis indrea Baldensperger, 1928: 173. *Lapsus calami*.
Apis johni Skorikov, 1929: 251.

Apis indica philippina Skorikov, 1929: 252.
Apis indica skorikovi Maa, 1944: 4. *Nomen nudum* (*vide skorikovi* Engel, 1999). [ICZN Article 13.1].
Apis mellifera gandhiana Muttoo, 1951: 153.
Apis (*Sigmatapis*) *lieftincki* Maa, 1953: 572.
Apis (*Sigmatapis*) *samarensis* Maa, 1953: 580.
Apis indica sinensis ussuriensis Goetze, 1964: 26. *Nomen nudum et invalidum* [ICZN Articles 10.2, 13.1, 15.2].
Apis cerana abansis Yang & Kuang, In Yang, Xu, Kuang, & Liu, 1986: 90. **Syn. nov.**
Apis cerana hainana Yang & Kuang, In Yang, Xu, Kuang, & Liu, 1986: 91. **Syn. nov.**
Apis cerana fantsun mountaina Zhuang, 1989: 61. *Nomen invalidum* [ICZN Articles 10.2, 15.2]. **Syn. nov.**
Apis cerana shenp countica Zhuang, 1993 [sic]: 61. *Lapsus calami*.
Apis ceran [sic] *cathayca* Zhuang, 1989: 62. **Syn. nov.**
Apis ceran [sic] *fantsan mountaina* Zhuang, 1993 [sic]: 62. *Lapsus calami*.
Apis ceran [sic] *sheng countica* Zhuang, 1989: 62. *Nomen invalidum* [ICZN Articles 10.2, 15.2]. **Syn. nov.**
Apis cerana pekinga Zhuang, 1989: 62. **Syn. nov.**
Apis cerana bijieca Zhuang, 1989: 62. **Syn. nov.**
Apis cerana kweiyanga Zhuang, 1989: 62. **Syn. nov.**
Apis cerana twolakeca Zhuang, 1989: 62. **Syn. nov.**
Apis cerana shankianga Zhuang, 1989: 62. **Syn. nov.**
Apis cerana himalaya Smith, 1991: 154. *Nomen nudum* (erroneous and invalid Latinization of informal term "Himalaya race" as applied by Ruttner, 1988: 121) [ICZN Article 13.1].
Apis cerena Willis, Winston, & Honda, 1992: 169. *Lapsus calami*.
Apis cerana himalayana Ruttner, 1992: 296. *Nomen nudum* (misspelling of already invalid name *himalaya* Smith, 1991). [ICZN Article 13.1]
Apis cerana twolareca Chen, 1993: 21. *Lapsus calami*.
Apis cerana heimifeng Engel, 1999: 179. **Syn. nov.**
Apis cerana skorikovi Engel, 1999: 180. **Syn. nov.**
Apis cerana abaensis Hepburn, Smith, Radloff & Otis, 2001: 6. *Nomen nudum et invalidum*, *et nomen vanum* [ICZN Articles 13.1, 16.1, 16.4, 33.2.3]. **Syn. nov.**
Apis cerana hainanensis Hepburn, Smith, Radloff & Otis, 2001: 6. *Nomen nudum et invalidum*, *et nomen vanum* [ICZN Articles 13.1, 16.1, 16.4, 33.2.3]. **Syn. nov.**

4. DISCUSSION

4.1. Trinomial names

Trinomial epithets (e.g. *Apis cerana cerana*) represent a historical artefact of earlier nomenclatural systems and can create considerable confusion when applied in modern systems. While prior to 1969 such names were usually applied for extreme forms of variation, more modern applications of trinomial names have been for ranges of variation (and not necessarily a single variant) over a specified geographic region. Thus, while the names can be used to refer to a circumscribed cluster within a variable species [as they are meant under rules of the ICZN, 4th Edition, 1999], often they are misapplied and collapse back into older systems of use. Rather than revising and updating the system of names, subsequent authors perpetuated this historical artefact and by the end of the 20th century, some 31 putative "taxa" of *A. cerana* had been established (Hepburn et al., 2001a), although many were not valid under modern ICZN rules (e.g., briefly summarized by Engel, 1999). The question must be asked: how did these "names" come about and are any of them actually biologically meaningful? The short answer is that all of these trinomials arose as artefacts of sampling coupled with the use by honey bee researchers of long out-dated taxonomic procedures.

According to modern taxonomic practice none of the "formal" Latin names historically applied to variations in *Apis* would be considered suitable, and many are not even legitimate. As such, those that were validly established under the nomenclatural rules of

their day should be accordingly recognized as synonyms. Similarly, the remaining, largely post-1970, names also should be considered synonyms, with the caveat for several that they were invalidly established under any taxonomic concept. Detailed synonymic summaries in standard taxonomic format for *A. cerana* are given in Engel (1999). As a consequence of these published synonymies, trinomials such as *A. c. japonica* or *A. c. cerana* no longer have any official, nomenclatural standing in *Apis* classification and under the rules of the ICZN. All former subspecies simply fall into disuse. By the same token, the morphocluster names such as "Himalayan *cerana*" or "Indo-Malayan *cerana*", as we propose are not binding, but offer *Apis* biologists an alternative solution in which the contiguous populations of *A. cerana* can be sensibly separated in what is still a biologically meaningful way.

4.2. Constraints on *A. cerana* morphoclusters

The interactive effects of limited sampling coupled with the Linnean system of nomenclature have shaped the historical process of unravelling the *A. cerana* complex. The importance of sample size, sample characters and inter-locality sampling distances has now been resolved (Radloff and Hepburn, 1998). In a series of regional parallel studies on the *A. cerana* of China, Tan Ken et al. (2002, 2003) showed that bees from the northern high-altitude areas of Yunnan Province were clearly larger and darker, and showed similarities with samples from Beijing, Nepal and north India, whereas bees from southern Yunnan clustered with the bees from Thailand and Vietnam. These results are completely consistent with those of Radloff et al. (2005b) for the bees of southern Yunnan. Morphometric analyses of *Apis cerana* from oceanic Asia yielded two distinct morphoclusters: (1) the bees of Japan and (2) the bees of all the other south Asian islands bringing the then total number of morphoclusters to seven (Radloff et al., 2005c). On completion of the above series of regional mesoscale studies, the newly formed comprehensive data set for all *A. cerana* was subjected to multivariate morphometric analysis. The final result is that six morphoclusters of *A. cerana* were obtained (Fig. 1).

When all of the mesoscale morphoclusters of the present authors are compared with the new macroscale results, the only discrepancies are that in the former (1) the bees of the Philippines were included with those of Indonesia and Borneo and (2) the bees of Japan are now placed in the Northern Asia morphocluster of the latter. However there are differences between the mapped morphocluster results of Ruttner (1988), Damus and Otis (1997) and our present ones. These discrepancies are best explained by sampling differences in each study, which affected the degree of morphometric discrimination of the honey bees of Japan. Ruttner (1988) only had access to a very small sample of large *A. cerana* from China and none from Russia. The only Morphocluster I bees available to him were from the far northwest of the *A. cerana* range (Afghanistan and Pakistan) and some 6000 km distant from Japan, the bees of which form a subcluster in a continuum of *A. cerana* Morphocluster I. Gaps in sampling inevitably resulted in the differences between Afghani and Japanese *A. cerana* being statistically magnified. The dataset of Damus and Otis (1997) was based on the much smaller bees of the more southerly oceanic islands (Philippines, Indonesia, Borneo, etc.) with the same effects. The data of Tan et al. (2008) is entirely consistent with that presented here.

4.3. Biogeography

A. cerana naturally occurs on an Asian landscape of some 30 M km^2 encompassing a series of climatic zones from tropical moist rainforest, wet-dry tropical savanna, mid-latitude steppe, dry mid-latitude grasslands, moist continental deciduous forest and taiga (Köppen Climate Classification System – cf. Müller, 1982). It is of interest to note how the distributions of the different morphoclusters and, possibly of subclusters within them, may be related to these various physiographic and climatic factors. The Philippine V and Indo-Malayan VI Morphoclusters both

lay below the South China Sea in the tropical wet climatic zone, yet are morphometrically differentiated. Reproductive isolation among them can be interpreted in a geological context (Voris, 2000). Palawan bees are in morphocluster VI and link with bees from Borneo which is not surprising because the sea depth between Borneo and Palawan is much shallower than between Palawan and the other 3 Philippine islands (Voris, 2000).

During the last 250 KBP of the Pleistocene, the Philippines were physically separated from the Indo-Malayan region about 75% of the time, clearly allowing differentiation through genetic drift. Differentiation into biometric subclusters within the Philippine group among the major islands systems reflects that they too were physically separated for 70% of the 250 KBP. In stark contrast, the bees of the Indo-Malayan morphocluster occur in the Indonesian chain of islands on islands that have been connected 50% of the last 250 KBP and nearly 70% of the last 17 K (Voris, 2000), which clearly forms a genetically more panmictic population. These geological data are completely consistent with the Euclidean linkage distances between these two oceanic morphoclusters.

Proceeding to the continental mainland, land links between the Indo-Malayan (VI) and Southeast Asian (IV) Morphoclusters resulted from lowered sea levels nearly 50% of the last 250 KBP and nearly 70% of the last 17 KBP, but there were never land connections between them and the Indian subcontinent. Here the Euclidean linkage distances provide a trend in the right direction. Nonetheless, there is a sharp transition between Indo-Malayan VI and the Southeast Asian Morphocluster IV, from a tropical dipterocarp rain forest to mixed moist deciduous forest with a wet and dry tropical climate to the northeast of the Isthmus of Kra in the northern Thai Malay Peninsula (Hughes et al., 2003). The rain forests actually extend up the western side of the isthmus along the Chin Hills-Arakan Yoma forests running between Myanmar and Bangladesh, the Naga Hills of India, the highlands of northern Laos and Chuor Phnum of Cambodia. These ecological discontinuities probably provide physiographic and ecological boundaries between the Southeast Asian IV and the adjoining eastern edge of the sub-Himalayan Morphocluster II.

The sub-Himalayan (II) and Southeast Asian (IV) Morphoclusters are adjacent in terms of their Euclidean linkage distances and subtend northern Morphocluster I along the Himalayas and then give way to a complex range of mountains (Hengduanshan, Wuliangshan, Taniantawengshan, Nushan and Qingshuilangshan), which turn southwards along the present Myanmar-China border. The sub-Himalayan morphocluster contains two recognizable subclusters, the larger Indus and smaller Ganges populations. The morphometric distinctness of these two populations arises from the fact that they differ significantly in the seasonal timing of reproductive swarming (Hepburn et al., 2001b).

Northern Morphocluster I extends over the largest land areas where *A. cerana* occurs (Fig. 1) and consists of six biometrically definable subclusters. The Indus population (Morphocluster I) occurs in a tropical wet and dry climate while its northwestern neighbour, the Himachali population occurs in the subtropical steppe. These climatic differences provide a degree of reproductive isolation between the populations because of seasonal differences in swarming so reducing the possibility of gene flow between them (Muzaffar and Ahmad, 1989; Saraf, 1985; Sharma, 1960). The Himachali population is also largely isolated from the eastern (north and south) Chinese subclusters by the intervening subarctic climate of the Tibetan highlands. Moving eastwards, the next populations of Morphocluster I are the northerly Aba and central and eastern China and Japonica biometric subclusters. The Aba area is in a subtropical mountain system while that of the central and eastern China and Japonica subclusters are situated in subtropical humid forest. The Aba and central and eastern subclusters have only partial overlap in seasonal swarming (Gong, 1983; Liu and Lai, 1990; Zhu, 1996). The South China subcluster (S Yunnan, Hainan, Guangdong, Guangxi) is essentially tropical.

As a final observation, it can be noted that *A. cerana* has been introduced to areas where it did not occur. In the 19th century it

was introduced into the northeastern provinces of Heilongjiang and Jilin, China from maritime Russia (Chen, 1993). Likewise it has been introduced to Ambon Island to the east of Sulawesi (Maa, 1953) as well as Iran (Gassparian, 1977). That *A. cerana* is an invasive species is evident from the fact that it was introduced from Java into Papua New Guinea in the late 1970's and now occurs throughout New Guinea (Anderson, 1989). From there it has reached islands in the Torres Strait (Dunn, 1992) and even more recently New Britain and the Solomon Islands (Anderson, 2005 – unpublish. data). *A. cerana* from Papua New Guinea are morphometrically indistinguishable from those of Java (Radloff et al., 2005c). It has also been intercepted several times at Darwin, Brisbane and near Perth, Australia.

Structure de la population et classification d'*Apis cerana*.

***Apis cerana* / sous-espèce / biogéographie / analyse morphométrique**

Zusammenfassung – Populationsstruktur und Klassifikation von *Apis cerana*. In diesem Artikel berichten wir über die Ergebnisse einer über das gesamte Verbreitungsgebiet reichenden multivariaten morphometrischen Analyse von *Apis cerana* und die statistisch definierten Morphokluster und Subklusterpopulationen innerhalb dieser. (1) Morphokluster I, „nördliche *cerana*", erstreckt sich vom nördlichen Afghanistan und Pakistan durch das nordwestliche Indien über das südliche Tibet, das nördliche Myanmar, China und dann nordöstlich nach Korea bis zum fernöstlichen Russland und Japan; (2) Morphokluster II, „himalaya *cerana*" schließt die Bienen des nördlichen Indien und einige Regionen des südlichen Tibet und Nepal ein. (3) Morphokluster III „indische Ebene *cerana*" besiedelt die Ebenen des zentralen und südlichen Indien und Sri Lanka. (4) In Morphokluster IV, „indo-chinesische *cerana*" gruppieren sich die Bienen von Myanmar, Nordthailand, Laos und Südvietnam; (5) Morphokluster V „philippinische *cerana*" ist auf die Philippinen beschränkt; (6) Morphokluster VI, hier als „indo-malayische *cerana*" bezeichnet, erstreckt sich von Südthailand über Malaysia und Indonesien. Wir stellen die Beziehungen der Morphokluster untereinander und ihre geophysikalischen und ökologischen Umgebungen dar und erstellen eine neue Verbreitungskarte auf Grundlage der gesamten über *A. cerana* publizierten Literatur (Hepburn and Hepburn, 2006). Einige Anmerkungen zu Genfluss und zeitlicher reproduktiver Isolation werden aus Daten zu Schwärmen und Wanderungen abgeleitet.
Nach moderner taxonomischer Praxis sind keine der historisch verwendeten "formellen" lateinischen Namen für die Variationen von *Apis* passend oder legitim. Daher sollten die Namen unter den Nomenklaturregeln ihrer Zeit gültig erstellten Namen sowie auch die übrigen, überwiegend nach 1970 erstellten Namen als Synonyme angesehen werden. Eine detaillierte synonymische Zusammenstellung im standardisierten taxonomischen Format findet sich bei Engel (1999). Als Konsequenz dieser publizierten Synonyme sind Trinomen wie *A. c. japonica* oder *A. c. cerana* unter den Regeln der ICZN keine offiziellen Bestandteile der Klassifikation von *Apis* mehr. Alle früheren Unterarten sind damit außer Gebrauch. Im gleichen Sinne sind Namen der Morphokluster wie „himalaya *cerana*" und „indo-malayische *cerana*" wie wir sie hier gebrauchen nicht bindend, sie bieten Bienenwissenschaftlern aber eine weitere Möglichkeit, die zusammenhängenden Populationen von *A. cerana* sinnvoll und biologisch begründet zu unterteilen. Die ICZN Zusamenfassung der Taxonomie für *A. cerana* ist hier zusammen mit der formellen Synonymie der Unterartnamen und anderen Namen zusammengestellt, wie es von der Nomenklatur gefordert wird.
Zuletzt soll angemerkt werden, dass *A. cerana* in das nordöstliche China, nach der Ambon Insel, Iran und papua-Neuguinea eingeführt wurde. Von dort hat sie Inseln in der Torresstraße besiedelt (Dunn, 1992) und in neuerer Zeit Neubritannien und die Salomoninseln erreicht (Anderson, 2005 – unpubl. data). *A. cerana* von Papua-Neuguinea sind morphologisch von denen aus Java nicht unterscheidbar. *A. cerana* wurde darüber hinaus mehrere Male in Darwin, Brisbane und nahe Perth, Australien aufgegriffen.

***Apis cerana* / Unterarten / Morphometrie / Biogeographie**

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