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Original article

The morphometric position of *Apis nuluensis* Tingek, Koeniger and Koeniger, 1996 within cavity-nesting honey bees

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Summary — Morphological features of nine samples of *Apis nuluensis* collected at the region of Sabah, Borneo, Malaysia in mountainous areas ranging from 1 524 to 3 400 m were analysed using 38 characteristics. Seventeen measurements of sizes, ten of coloration and hairyness, and 11 of wing venation angles were measured according to the methods of Ruttner et al (1978). The morphological position was evaluated within a frame containing other cavity-nesting *Apis* species drawn from the Oberursel data bank (*Apis cerana* from four Asian locations, *Apis koschevnikovi*, *Apis nigrocincta* and two equatorial *Apis mellifera* races). *A nuluensis* shows some extreme characteristics which separate it from all other cavity-nesting bees, or all *A cerana* groups. In size measures it is closest to *A nigrocincta* from Sulawesi, while wing venation measures are close to the northern *A cerana* groups. Factor analysis showed *A nuluensis* to be clearly and significantly distinct from each of the other groups on at least two of the first three principal component axes. In discriminant analysis, all *A nuluensis* samples were assigned to their group with high probability. In particular, *A nuluensis* clearly differed from the sympatric groups, *A cerana* from Borneo and *A koschevnikovi*. In relation to *A cerana* in general, and to the sympatric *A cerana* from Borneo, this distinctness is less pronounced than that of *A koschevnikovi*, while the results from wing venation angles alone gave the opposite result.

***Apis nuluensis* / morphometry**

INTRODUCTION

Tingek et al (1996) described *Apis nuluensis* Tingek, Koeniger and Koeniger, 1906, a new species of cavity-nesting honey bee. These were first collected on flowers at altitudes above 1 500 m, and recognized as morphologically distinct. In collection sites where *Apis cerana* was found, the absence of intermediates between the forms indicated reproductive isolation, which was confirmed by Koeniger et al (1996). While Tinkek et al described the characteristic morphological features of the new species,

this study aims to determine the morphometric position of this new species, in relation to *A cerana* from a wide range of locations, to the sympatric species *Apis koschevnikovi*, and to *Apis mellifera* from equatorial origin.

MATERIALS AND METHODS

Nine samples of *A nuluensis* were used. Bees had been sampled at the region of Sabah, Borneo, Malaysia in 1994 and 1995 in mountainous areas (height range 1 524 to 3 400 m). Eight of the samples were collected from flowers and contained 11.1 workers on average (range 2–18), one sample contained bees from one colony (30 workers). Samples were identical to those used by Tingek et al (1996). Bees were dissected and measured according to the methods described by Ruttner et al (1978). Thirty-eight morphometric characteristics (17 characteristics of size, ten characteristics of coloration and hairyness, 11 characteristics of wing venation angles) were measured, using a stereomicroscope and a CCD-camera with a PC on-screen digitizing system (Meixner, 1994).

Samples of cavity-nesting bees from the morphometric data bank in Oberursel were used for comparison. These included *Apis cerana indica* from Borneo (24 samples, 11 from the western region of Sabah, 13 from the south-eastern region of Sabah) and from Sri Lanka (five samples), *Apis cerana cerana* from China (nine samples from the region of Bejing) and *Apis cerana japonica* from Japan (eight samples, four from Tokyo, four from Nagasaki). Further included were ten samples of *Apis nigrocincta* F Smith from Sulawesi, which were the same as those analysed by Hadisoesilo et al (1996), *A koschevnikovi* (ten samples from Sabah/Borneo) and *A mellifera* from equatorial locations (*Apis mellifera scutellata*, ten samples, three from Tanzania, seven from Kenya; *Apis mellifera monticola*, eight samples from Kenya). All these samples contained between 15 and 20 workers.

All calculations were performed on the sample means, which reflect means of sampling locations in eight of the nine *A nuluensis* samples, and means of colonies in all other samples. Data were analysed by factor analysis and discriminant analysis. Group positions on three principal component factor score axes were compared by ANOVA and LSD tests. Euclidian distances between group centroids were calculated from discriminant analysis and were clustered. All tests were performed using SPSS for Windows (version 6.0, 1993).

RESULTS

Direct comparison of the morphometric characteristics showed some characteristic features of *A nuluensis*. In four of the traits, *A nuluensis* had an extreme position where its values were either the highest or the lowest of the groups (table I; angles G18 and L13: lower; angle N23: higher; distance between wax mirrors: higher). In one trait (pigment of scutellum 1) *A nuluensis* showed the lowest value compared with all the other groups except *A m monticola*, and had the highest value in the width of the dark stripe of the tomentum compared with all the other groups except *A koschevnikovi*. In six of the size-related measures, *A nuluensis* ranged between the southern and the northern *A cerana* groups and differed significantly from each of these at a minimum level of $P = 0.05$ (ANOVA, LSD test).

In ten of the 38 measures, *A nigrocincta* was closest to *A nuluensis*, nine of these were size-related. The same applied to four of the nine derived measures, in particular body size and leg size. In eight of the eleven wing venation angles, *A nuluensis* was closest to the northern *A cerana* groups, *A cerana cerana* from China (four) or *A c japonica* from Japan (four).

In factor analysis, the first three main factors explained 70% of the variance (38.6, 21.4 and 9.8%, respectively). In the rotated factor matrix, factor 1 showed a high correlation ($|r| > 0.6$) with size-related measures (sizes: 15), factor 2 with wing venation, hairs and pigments (wing venation angles: 6; hairs / pigments: 4) and factor 3 predominantly with pigmentation (pigments: 4, wing venation angles: 1).

Table I. Mean values and standard deviations for some of the measured characteristics, or of derived characteristics.

	A nuluensis	A koschevnikovi	A nigrocincta *(Sulawesi)*	A cerana *(Borneo)*	A cerana *(Sri Lanka)*	A cerana *(China)*	A cerana *(Japan)*	A m scutellata	A m monticola
Sample size	9	10	10	24	5	9	8	10	8
Body size	3.72 ± 0.05	3.97 ± 0.05***	3.71 ± 0.08^{ns}	3.39 ± 0.05***	3.25 ± 0.05***	4.02 ± 0.09***	4.03 ± 0.06***	3.94 ± 0.16**	3.98 ± 0.13**
Leg	7.38 ± 0.04	7.64 ± 0.05***	7.31 ± 0.12^{ns}	6.65 ± 0.08***	6.58 ± 0.09***	7.64 ± 0.11***	7.67 ± 0.08***	7.35 ± 0.28^{ns}	7.44 ± 0.23^{ns}
Body size/leg	0.50 ± 0.006	0.52 ± 0.005***	0.58 ± 0.006^{ns}	0.51 ± 0.004*	0.49 ± 0.008*	0.53 ± 0.007***	0.53 ± 0.011***	0.054 ± 0.017***	0.054 ± 0.017**
Slenderness	0.82 ± 0.011	0.86 ± 0.028***	0.80 ± 0.018*	0.81 ± 0.018^{ns}	0.87 ± 0.016***	0.82 ± 0.013^{ns}	0.81 ± 0.016^{ns}	0.87 ± 0.045**	0.86 ± 0.041*
Angle G18	88.0 ± 1.1	93.8 ± 1.5***	90.3 ± 1.8***	90.2 ± 1.6***	95.0 ± 1.8***	92.2 ± 1.9***	90.0 ± 0.9***	97.4 ± 1.6***	94.8 ± 1.9***
Angle L13	11.0 ± 0.4	15.0 ± 1.9***	13.7 ± 0.6***	14.0 ± 0.6***	14.8 ± 1.0***	14.3 ± 0.5***	15.0 ± 0.7***	14.5 ± 1.7***	13.2 ± 0.7***
Angle N23	90.5 ± 1.3	86.0 ± 2.8***	78.1 ± 2.28***	85.7 ± 1.0***	83.1 ± 2.2**	82.7 ± 1.4***	78.1 ± 2.1***	87.5 ± 2.9*	87.6 ± 2.5*
Distance wax mirror	0.46 ± 0.01	0.30 ± 0.03***	0.43 ± 0.03***	0.36 ± 0.02***	0.29 ± 0.03***	0.32 ± 0.02***	0.29 ± 0.02***	0.32 ± 0.03***	0.34 ± 0.04***
Pigment scutellum 1	3.7 ± 1.36	7.19 ± 0.61***	7.09 ± 0.10***	6.30 ± 0.74***	6.33 ± 0.89**	5.62 ± 1.72**	5.25 ± 1.91^{ns}	4.80 ± 0.94^{ns}	0.99 ± 0.78***
Dark stripe tomentum	0.89 ± 0.03	0.98 ± 0.04***	0.76 ± 0.02***	0.80 ± 0.02***	0.55 ± 0.09***	0.75 ± 0.09**	0.64 ± 0.19***	0.55 ± 0.07***	0.67 ± 0.05***

Measures of sizes are given as mm, angles as degrees. Body size = sum of length of tergite 3 and 4; leg = sum of hind femur, tibia and metatarsus; Slenderness = length/width of sternite 6. Significance of differences to *A nuluensis*: * $P < 0.05$, ** $P < 0.005$, *** $P < 0.0005$.

Figure 1 shows a three-dimensional plot of the factor scores on the first three principal component axes. The positions of the groups differed significantly on all three axes (ANOVA, $P < 0.000\ 05$). All of the 28 possible pairs differed on at least one of the axes ($P < 0.05$, LSD test), and were thus all separate. One was not different on two axes: *A koschevnikovi* and *A cerana* (China), axes 1 and 2. Eleven pairs were not separable on one of the axes. *A nuluensis* was separable from all groups on all axes except from *A nigrocincta* from Sulawesi on axis 1 and from *A m monticola* on axis 3. A factor analysis restricted to wing venation angles separated all groups except the two *A m* groups on at least one of the axes and thus confirmed the above results. *A nuluensis* sample means were different from all other groups on all three 3 axes, except from *A koschevnikovi* on axis 1.

In discriminant analysis, 98.9% of the samples were assigned to their correct groups. One *A cerana* sample from Borneo was misplaced into the *A nuluensis* group. All assignments had a probability of $P > 0.99$. All of the *A nuluensis* samples were correctly assigned to their group with $P > 0.99$. When forced to be classified into the other groups, all *A nuluensis* were assigned to *A cerana* from Borneo with $P > 0.99$. Similar results were obtained using wing venation angles only. Some 99% of the samples were assigned to their correct groups (one *A m monticola* was placed in the *A m scutellata* group), 92.4% with $P > 0.95$. All *A nuluensis* samples were assigned

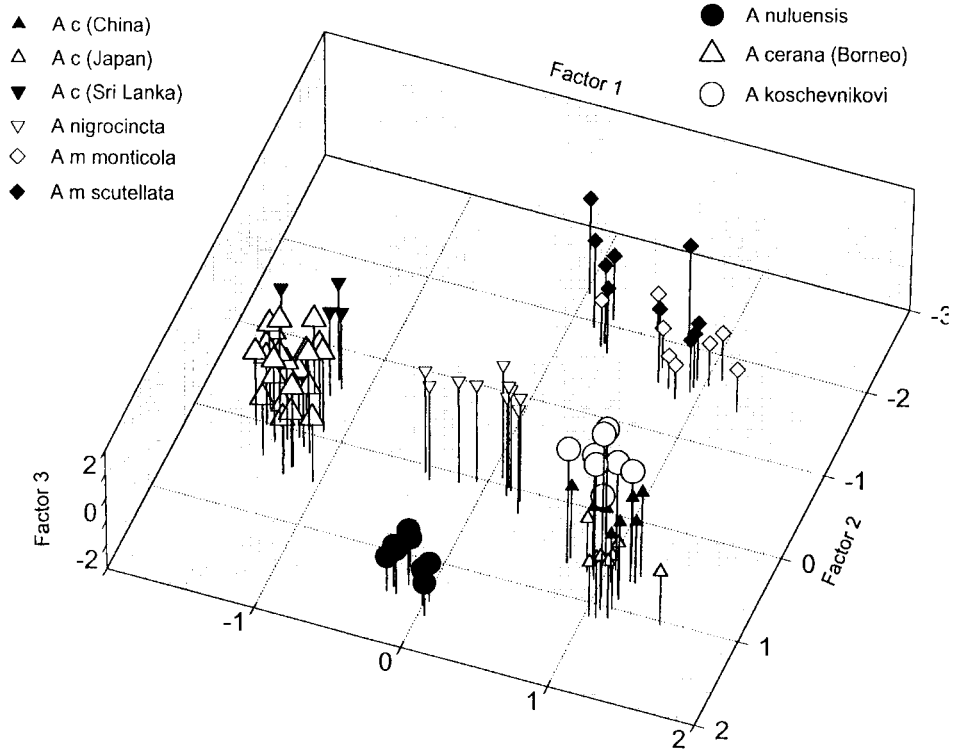

Fig 1. Factor analysis of the cavity-nesting *Apis* groups, plotted on the first three PCA axes. The groups sympatric with *A nuluensis* are signified by big symbols. *A c* = *A cerana*, A m = *A mellifera*.

to their group with $P > 0.99$ and none of the other samples were included. If forced to be classified, one *A nuluensis* would have been assigned to *A cerana* from Borneo with $P = 0.68$, the other nine to *A cerana* from China with $P > 0.95$.

Euclidian distances between group centroids were calculated within the eight-dimensional canonical discriminant axes space. In relation to the *A cerana* group, *A nuluensis* is nearest to *A cerana* from Borneo (fig 2, ordinate), closely followed by *A cerana* from China and Japan. *A nigrocincta* and *A koschevnikovi* are somewhat more distant than the previous groups, but still closer than *A cerana* from Sri Lanka. The *A mellifera* bees are clearly quite distant. If only wing venation angles are considered, *A nuluensis* is closer to *A cerana* from China (6.1) and Japan (7.6) than to *A cerana* from Borneo (8.0) and *A koschevnikovi* (8.7), and also closer to *A cerana* from Sri Lanka (9.2) than to *A nigrocincta* (11.1).

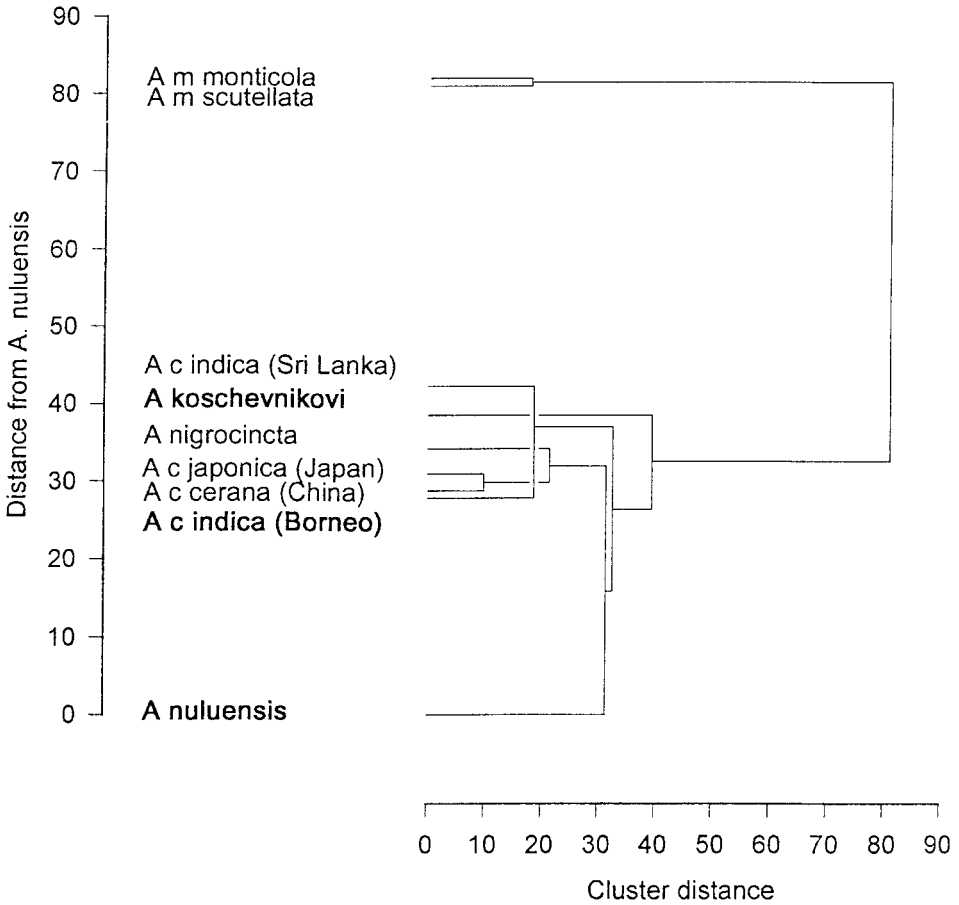

Fig 2. Hierarchic cluster analysis of group centroids in canonical discriminant function space. *A c* = *Apis cerana*, A m = *A mellifera*. Ordinate: distance of other cavity-nesting *Apis* groups from *A nuluensis*. Abscissa: cluster distance at the agglomeration steps. Groups sympatric with *A nuluensis* are marked in bold print.

In the three sympatric bees, *A nuluensis* is about one quarter closer to *A cerana* from Borneo than to *A koschevnikovi* (27.8 and 38.5, respectively). These in turn are more distant to each other (d = 48.2, not to be seen from the graph). If only wing venation angles are considered, *A nuluensis* is about equidistant to *A cerana* from Borneo than to *A koschevnikovi* (8.0 and 8.7, respectively), with a relatively smaller distance between *A cerana* from Borneo and *A koschevnikovi* (6.0).

To visualize the general proximity relations, the distances were clustered. The sequence of agglomeration is also shown in figure 2, with the cluster distances given at the abscissa. Clustering shows two main branches of *A cerana*, one combining *A cerana* bees from China and Japan with *A nigrocincta* from Sulawesi, the other those from Borneo and Sri Lanka. *A nuluensis* is joined to the first group at about the same distance the two *A cerana* groups are linked. *A koschevnikovi* is connected in the next step, followed at a high distance by the *A mellifera* cluster. If the analysis is restricted to wing venation angles, results differ in that *A koschevnikovi* is integrated into the *A cerana* cluster, while *A nuluensis* is joined from a clearly higher distance as the last group until the *A mellifera* cluster is joined.

DISCUSSION

Tingek et al (1996) established *A nuluensis* as a new honey bee species, and described characteristic morphological features. *A nuluensis* is reproductively isolated from the sympatric species by performing mating flights at a different time of day (Koeniger et al, 1996). The morphometric comparison based on 38 characteristics underlines the distinctness of the species. Some particular features separate *A nuluensis* from other cavity-nesting *Apis* species, including a group as distant as equatorial *A mellifera*. These were the extreme distance between the wax mirrors, already noted by Tingek et al (1996), and the extreme values of three of the wing venation angles. From the other *A cerana* groups and particularly from *A koschevnikovi* and *A nigrocincta, A nuluensis* is set apart by the dark pigmentation of scutellum 1, and from the *A cerana* groups by the wide dark stripe between the tomentum and the posterior rim of the tergite 4. Factor analysis and discriminant analysis confirmed the clearly separate position of this bee in the morphometric space in analysis including all or only size-independent wing venation measures.

A nuluensis is a medium-sized cavity-nesting honey bee. Measurements of body size features were generally between that of the *A c indica* and the northern *A cerana* groups. In the majority of the size measures *A nuluensis* was closest to *A nigrocincta* from Sulawesi, whose systematic status as a species was confirmed by Hadisoesilo et al (1996) and Otis (1996). *A nuluensis* is nevertheless clearly different from this *A nigrocincta* in other respects, eg, it occupies the opposite end of the range concerning the pigmentation of scutellum 1 and scutellum 2. Also it was unequivocally separated by the different multifactorial methods. If only wing venation is considered, the distance between these two groups was even more pronounced.

Clustering centroid distances separated the northern *A cerana* groups, *A c cerana* and *A c japonica*, from the southern *A c indica* groups. *A nuluensis* is joined to the *A cerana* clusters at about the same distance that these combine. *A nigrocincta* is closely linked to the northern *A cerana* branch, while *A koschevnikovi* is set apart and joins the cluster only later. This pattern seems to be at least partly influenced by size-related characteristics. In analysis based on wing venation alone, the *A cer-*

ana groups are clustered together with *A koschevnikovi* and *A nigrocincta* and *A nuluensis* is joined at a higher distance, appearing more akin to the northern than to the southern *A cerana* groups.

Arias et al (1996) constructed phylogenetic relations between cavity-nesting *Apis* species based on DNA sequences. They found *A nuluensis* to be closer related to the *A cerana* groups than *A koschevnikovi* and concluded that *A nuluensis* might be a more recently evolved sister taxon to *A cerana* than *A koschevnikovi*. The results of morphometric comparison, although different in some details, also showed a closer relation of *A nuluensis* to the *A cerana* groups than that of *A koschevnikovi*. This is particularly pronounced if only the sympatric *A cerana* from Borneo is considered where the distance to *A nuluensis* is only 62% of that to *A koschevnikovi*. These results would thus support the conclusion of Arias et al (1996). Their conclusion, however, is not supported in analyses based on wing venation alone, which produces a clear distinction of *A nuluensis* from the other Asian groups, with a 133% higher distance from the sympatric *A cerana* population than that of *A koschevnikovi*. It is not clear why wing venation, as a size-independent measure, presumed to be less influenced by ecological conditions, yields results which differ from that of DNA-analysis methods while morphometric analysis based on all characters does not. This contradiction, however, does not allow us to draw conclusions about the relative antiquity of the sister taxons at this stage.

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Zusammenfassung — Die morphometrische Stellung von *A nuluensis* Tingek, Koeniger and Koeniger, 1996 innerhalb der höhlenbewohnenden Honigbienen. Die morphometrische Stellung der kürzlich entdeckten Honigbienenart *A nuluensis* Tingek et al (1996) wurde in Beziehung zu den anderen höhlenbewohnenden Honigbienenarten bestimmt. Die Analyse beruhte auf neun Bienenproben von *A nuluensis*, die in der Region von Sabah, Borneo, Malaysia in Höhenlagen von 1524 bis 3400 m gesammelt worden waren. Es wurden 38 morphologische Charaktere entsprechend den von Ruttner et al (1978) angegebenen Methoden ausgewertet. Dies waren 20 Größenmerkmale, 7 Färbungsmerkmale und 11 Winkel der Flügeläderung. Messungen der anderen höhlenbewohnenden *Apis*-Arten wurden der Datenbank von Oberursel entnommen (*A cerana indica* aus Borneo und Sri Lanka, *A cerana cerana* aus China, *A cerana japonica* aus Japan, *A nigrocincta* aus Sulawesi (Daten aus Hadisoesilo et al, 1996), *A koschevnikovi* aus Borneo und zwei äquatoriale Rassen von *A mellifera*. *A nuluensis* hat einige morphologische Besonderheiten, in denen sie extreme Messwerte aufweist. Dies sind der große Abstand zwischen den Wachsspiegeln und die extremen Werte von drei der Flügelwinkel (G18, L13, N23). Von den anderen Gruppen von *A cerana* und besonders von *A koschevnikovi* und *A nigrocincta* setzt sich *A nuluensis* durch die dunkle Pigmentierung von Scutellum 1, und von allen anderen Gruppen ausser *A koschevnikovi* durch die Breite des dunklen Streifens hinter den Filzbinden (Tom2) ab. In den Größenmerkmalen nimmt *A nuluensis* eine mittlere Position ein und befindet sich am nächsten zu *A nigrocincta* aus Sulawesi. Von dieser ist sie aber anson-

sten klar abgetrennt. In den Flügelwinkeln liegt sie am nächsten an den *A cerana*-Unterarten aus China und Japan. In der Faktorenanalyse zeigte sich *A nuluensis* auf mindestens zwei der drei Achsen deutlich und signifikant von jeder der anderen Gruppen gesondert. Die Ergebnis konnte auch bei Beschränkung auf die Flügelwinkel allein bestätigt werden. Die klare Trennung zwischen den Gruppen konnte auch durch Diskriminanzanalyse nachvollzogen werden, sowohl auf Grundlage aller Merkmale oder mit den Flügelwinkeln allein. Alle *A nuluensis* konnten hierbei ihrer korrekten Gruppe mit hoher Wahrscheinlichkeit zugeordnet werden ($P > 0.99$). Auf der Grundlage einer Clusteranalyse der Zentroidabstände aus der Diskriminanzanalyse liegt *A nuluensis* morphometrisch näher bei *A cerana*, und insbesondere bei der sympatrischen *A cerana* aus Borneo, als bei der anderen taxonomischen Geschwistergruppe, *A koschevnikovi*. Diese Beziehung ist allerdings in ihr Gegenteil verkehrt, sobald ausschließlich die Flügelwinkel einbezogen werden.

***Apis nuluensis* / Morphometrie**

Résumé — La position d'*Apis nuluensis* Tingek, Koeniger et Koeniger, 1996 d'un point de vue morphologique au sein des abeilles mellifères qui nidifient dans des cavités. La position de l'espèce *A nuluensis*, récemment découverte, a été déterminée sur le plan de la morphologie par rapport aux autres espèces d'*Apis* qui nidifient dans des cavités. L'analyse a porté sur neuf échantillons d'*A nuluensis* prélevés sans la région de Sabah, à Bornéo (Malaysia), dans des régions montagneuses, entre 1 524 et 3 400 m. Trente-huit caractères morphologiques ont été mesurés selon les méthodes de Ruttner et al (1978) : 20 mesures corporelles, sept mesures de la coloration et 11 d'angles de la veination alaire. Pour les autres espèces d'*Apis* (*A c indica* de Bornéo et de Sri Lanka, *A c cerana* de Chine, *A c japonica* du Japon, *A nigrocincta* identifié par Hadisoesilo (1996), *A koschevnikovi* de Bornéo et deux races équatoriales d'*Apis mellifera*), les mesures suivantes ont été prises dans la banque de données d'Oberursel : plus grande distance entre les miroirs à cire et valeurs extrêmes des angles G18,L13 et B23 de la veination alaire. *A nuluensis* se sépare des autres groupes d'*A cerana*, et en particulier d' *A koschevnikovi* et d'*A nigrocincta*, par la pigmentation foncée du scutellum 1 et de tous les autres groupes, excepté *A koschevnikovi*, par la largeur de la bande foncée (Tom2). Pour les mesures corporelles, *A nuluensis* occupe une position intermédiaire et se rapproche le plus d'*A nigrocincta* du Sulawesi, dont elle se sépare très nettement par les autres facteurs. Pour les angles de la veination alaire, elle se situe le plus près des groupes septentrionaux d'*A cerana* de Chine et du Japon. L'analyse factorielle montre qu'au moins sur deux axes *A nuluensis* est nettement et significativement différente de chacun des autres groupes. L'analyse basée sur les angles de la veination alaire seuls confirme ce résultat. L'analyse discriminante sur tous les caractères ou sur les angles de la véntion alaire seuls confirme la séparation nette entre les groupes. Tous les échantillons d'*A nuluensis* ont été classés dans leur propre groupe avec une probabilité élevée ($p > 0,99$). D'après les résultats d'une méthode de classification portant sur les distances canoniques entre centroïdes issues d'une analyse discriminante, *A nuluensis* est plus proche, d'un point de vue morphologique, d'*A cerana* et en particulier d'*A cerana* sympatrique de Bornéo que de l'autre taxon sœur, *A koschevnikovi*. Cette relation est en revanche inversée si l'on considère les angles de la veination alaire.

***Apis nuluensis* / morphométrie**

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