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Original article

Morphometric analysis and biogeography of *Apis koschevnikovi* Enderlein (1906)*

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Abstract – Multivariate morphometric analyses were performed on workers of *Apis koschevnikovi* from throughout their distribution in Malaysia, Borneo and Indonesia. Principal component analysis showed one morphocluster comprising bees from Kalimantan Indonesia, Sarawak, Sabah and the Malay Peninsula. The population is more homogeneous than *A. cerana* over the same geographical area, as seen from the average coefficient of variation in 12 characters in *A. koschevnikovi* (1.8%) compared to those same characters in *A. cerana* (4.3%). *A. koschevnikovi* is delimited to the tropical evergreen forest regions of Sumatera, Borneo, and the Malay Peninsula (Fig. 1). The altitudinal distributions show that *A. koschevnikovi* extends from sea level to about 1600 m. This significantly differs from *A. nuluensis* but not *A. cerana.* It appears that the range of *A. koschevnikovi* is diminishing because it is now either poorly represented or absent in several areas where it has been previously recorded.

***Apis koschevnikovi* / morphometrics / distribution**

1. INTRODUCTION

Apis koschevnikovi was originally described by Enderlein (1906) as "*Apis indica* variety *koschevnikovi*" and also by von Buttel-Reepen (1906) as "*Apis mellifica indica* variety *koschevnikovi*". However, authorship for this species has been formally assigned to Enderlein (Engel, 1999). With the exceptions of Maa (1953) and Goetze (1964), there have been no other accounts of *A. koschevnikovi* from its original description until its rediscovery eight decades later in Borneo (Mathew and Mathew, 1988; Tingek et al., 1988). However, *A. koschevnikovi* had indeed been widely collected in the Sundaland region of Southeast Asia during the interim as evidenced by collections in various museums (Otis, 1997).

In a recent flurry of publications (cf. Hepburn and Hepburn, 2007), it was soon established that *A. koschevnikovi* is a morphometrically distinct species (Tingek et al., 1988; Rinderer et al., 1989; Ruttner et al., 1989; Sulistianto, 1990), that is reproductively isolated from (Koeniger et al., 1996), and differs in both nuclear and mitochondrial DNA regions (Arias et al., 1996; Takahashi et al., 2002; Raffiudin and Crozier, 2007) from other species of *Apis* with which it has a sympatric distribution.

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Here we report the results of multivariate analyses of morphometric variation in this species over its entire known range of distribution to define population structure and provide biogeographical information on and distribution maps for *A. koschevnikovi* in relation to *A. cerana* and *A. nuluensis* with which it is sympatric.

2. METHODS AND MATERIALS

2.1. Honeybees

Although most characters of length are some 10–15% greater in worker honeybees of *A. koschevnikovi* than in *A. cerana* (Rinderer et al., 1989; Sulistianto, 1990), these species may be confused in alcohol-preserved specimens that do not show the natural reddish-yellow brightness of the former. Workers of *A. koschevnikovi* are one of four medium-sized bees and may be quickly distinguished from them by the cubital index which is 7.64 ± 1.40 in *A. koschevnikovi*, 3.74 ± 0.24 in *A. cerana*, 4.25 ± 0.47 in *A. nigrocincta*, and 3.77 ± 0.12 in *A. nuluensis.*

The worker honeybees used in our study derive from: (1) data from bees collected in Sabah, Borneo (Malaysia), and Sumatera (Indonesia) from the database of the Institut für Bienenkunde at Oberursel, (Obeursel database, n = 13 colonies); (2) new data from bees collected from south Kalimantan Borneo (Indonesia), (Hadisoesilo-Raffiudin database, n = 30 colonies), and from the Malay Peninsula and Sarawak Borneo (Malaysia), (Grahamstown database, n = 5 colonies). Collectively, honeybees from 48 colonies representing 19 localities in Indonesia and Malaysia were measured morphometrically and statistically analyzed. In addition, published morphometric data on *A. koschevnikovi* from Rinderer et al. (1989), Sulistianto (1990), and Fuchs et al. (1996) were included for a complete analysis of this species. Finally, to compare the average coefficient of variation for *A. koschevnikovi* with that of *A. cerana* we used the same *A. cerana* island database published by Radloff et al. (2005).

The largest source of published locality data on the distribution of *A. koschevnikovi* is Otis (1997). Geographical coordinates and altitudes for identifiable localities in that dataset, plus all localities recoverable from all of the individual research papers (Hepburn and Hepburn, 2007) and new localities recently found by the present authors for *A. koschevnikovi* were used to prepare a new distribution map with GIS software (Fig. 1). The altitudes of all *A. koschevnikovi* localities and those of sympatric *A. cerana* (Hepburn and Hepburn, 2006) and *A. nuluensis* (Fuchs et al., 1996) were obtained and analyzed for pattern differences.

2.2. Morphometrics

Twenty-seven morphological characters of worker bees related to size or angles of venation were measured using the methods of Ruttner (1988) and the Ruttner parameters and their Ruttner numbers are given in brackets as follows: length of femur (5), length of tibia (6), metatarus length (7), metatarsus width (8), length of tergite 3 (9), length of tergite 4, (10), length of sternite 3 (11), length of wax plate of sternite 3, (12) width of wax plate of sternite 3 (13), distance between wax plates, sternite 3 (14), length of sternite 6 (15), width of sternite 6 (16), forewing length (17), forewing width (18), cubital a (19), cubital b (20), wing angle A4 (21), wing angle B4 (22), wing angle D7 (23), wing angle E9 (24), wing angle G18 (25), wing angle I10 (26), wing angle I16 (27), wing angle K19 (28), wing angle L13 (29), wing angle N23 (30), and wing angle O26 (31). The Grahamstown database consists of the following twelve morphological characters (5), (6), (7), (9), (10), (11), (12), (15), (17), B4 (22), D7 (23) and G18 (25).

2.3. Data analysis

Because the morphometric databases were derived from measurements by different people, to control for possible subjective error, an analysis of the databases from north Borneo (Oberursel) and south Kalimantan (Hadisoesilo-Raffiudin) was first performed, followed by an analysis of the

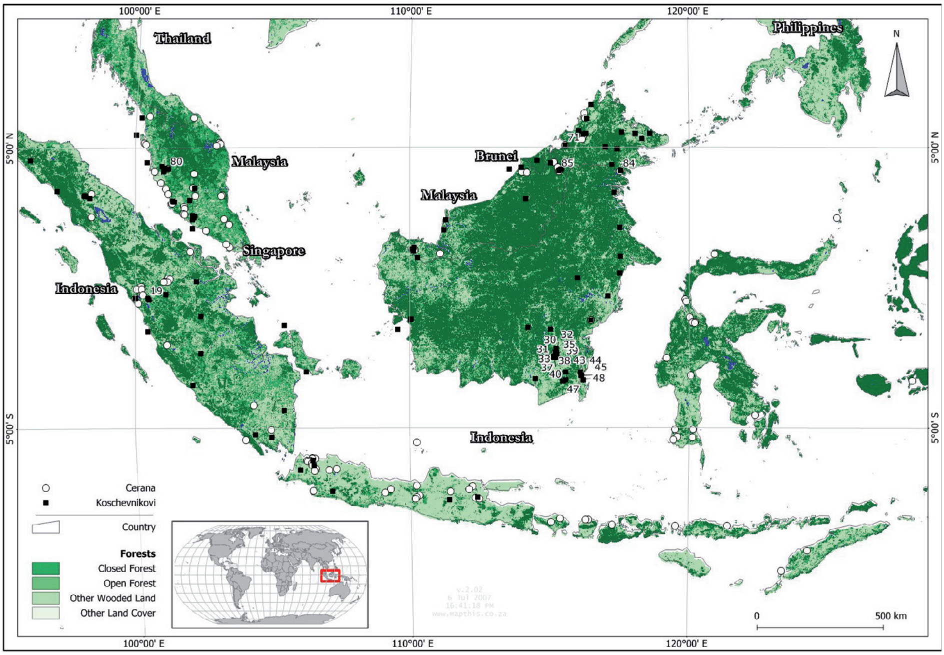

Figure 1. Geographical distribution of *A. koschevnikovi* and *A. cerana* based on all published records. Localities are given in Table I and additional online material.

combined Oberursel, Hadisoesilo-Raffiudin and Grahamstown databases.

Multivariate statistical analysis of the data included principal components, analysis of variance and Levene's F statistic procedures for testing heterogeneity of variances (Johnson and Wichern, 2002). A Bonferroni adjustment to the level of significance was used in order to ensure that the overall level of significance of the multiple comparison tests did not exceed $\alpha = 0.05$. Chi-square tests based on observed frequencies were used to compare the altitudinal distributions between species. All tests were performed using Statistica©(StatSoft, 2007).

3. RESULTS

3.1. Biogeography

Given sea level changes that connected the islands of Sundaland to the continent during much of the Pleistocene (Voris, 2000) and the current distribution of tropical evergreen rain forests in Southeast Asia, *A. koschevnikovi* might have been expected to extend well into the mainland. However, numerous excursions in tropical forests over the last decade in Thailand, Myanmar, Cambodia and Vietnam failed to find the species (S. Hadisoesilo, H.R. Hepburn, G.W. Otis, M. Pianchaeron, P.H. Thai, D.W. Roubik, S Wongsiri, all unpubl. data). It appears that *A. koschevnikovi* is probably restricted to the evergreen forests of the Malay Peninsula, Borneo and Sumatera. Moreover, further enquiries into geographical variation in *A. koschevnikovi* established morphometrically that *A. vechti vechti* of northern Borneo and *A. vechti linda* of Sumatera as described by Maa (1953) are only variations in *A. koschevnikovi* (Hadisoesilo et al., 1999).

The new data on the distribution of *A. koschevnikovi* establishes many new site localities but all within the previously defined limits of the tropical evergreen forest regions of Sundaland (Fig. 1, Tab. I and additional online material for the distribution of *A. koschevnikovi* based on all published

Table I. Distribution of localities, co-ordinates, altitude (m) of *A. koschevnikovi* where data are available, n = number of colonies.

Country & State/Province	Locality	Latitude	Longitude	Altitude	n
INDONESIA					
Sumatera	Tanjungampalo	0.22N	102.32E		1
Kalimantan	Jungkal	2.20S	115.25E	23	4
Kalimantan	Murung Jambu	2.31S	115.25E	25	1
Kalimantan	Abung	2.31S	115.27E	80	1
Kalimantan	Barabai	2.34S	115.22E	101	4
Kalimantan	Haliyau	2.38S	115.26E	50	2
Kalimantan	Hulu Muka	2.49S	115.17E	14	5
Kalimantan	Panggungan	2.49S	115.24E	100	1
Kalimantan	Lumpage	2.49S	115.25E	134	2
Kalimantan	Jelatang	2.50S	115.18E	28	1
Kalimantan	Benua Lama	3.02S	115.58E	30	1
Kalimantan	Berangas	3.14S	116.13E	29	3
Kalimantan	Tirawan	3.14S	116.15E	72	1
Kalimantan	Kersik Putih	3.29S	115.59E	35	2
Kalimantan	Serakaman	3.29S	116.21E	45	2
MALAYSIA					
Sabah	Tenom	5.07N	115.57E	500	9
Peninsula	Ringlet	4.24N	101.22E	1135	2
Sarawak	Tawau	4.15N	117.54E	0	3
Sarawak	Long Semado	4.15N	115.34E	858	3

records). The altitudinal distributions show that *A. koschevnikovi* mainly occurs between sea level and about 1200 m: for 102 recorded localities, 98 were < 1200 m, and 4 between 1200 to 2700 m. The 4 latter samples may have been confused with *A. nuluensis* (see additional online material for the distribution of *A. koschevnikovi* based on all published records). These altitudinal distributions are not significantly different from those of sympatric *A. cerana* (χ^2 = 6.9, df = 3, P = 0.0764), but are significantly different from those of geographically sympatric *A. nuluensis* for which only three localities have been reported and all are > 3000 m (χ^2 = 104.0, df = 3, P < 0.0001).

3.2. Analysis of the databases from north Borneo (Oberursel) and south Kalimantan (Hadisoesilo-Raffiudin)

All morphometrical characters passed tests of normality (Kolmogorov-Smirnov: 27 characters with P > 0.20) and homogeneity of the variances between colonies from northern Borneo and southern Kalimantan (Levene: 27 characters with P > 0.20). Univariate ANOVA results showed significant mean differences between the northern and southern groups in 9 of the 27 morphometric characters, namely size-related characters (9) to (14), cubital b (20) and angles of venation (27) and (31) (Tab. II). The colony means and standard deviations of 27 morphometric characters, together with cubital index, body size and character ratios averaged for the northern and southern groups are shown in Table II.

A principal components analysis was performed using the colony means of 27 morphometric characters of worker honeybees. Eight principal components with eigenvalues greater than one were isolated: PC 1, size-related characters (5), (6), (7), (8), (9), (10), (11), (13), (17), and (18) with component loadings between 0.62 and 0.78 accounting for 23.8% of the variation; PC 2, size-related character (12) and angle of venation O26 (31) with component loadings 0.79 and 0.74 accounting for

Table II. Means and standard deviations of 27 morphological characters (Ruttner (1988) numbers are given in brackets), together with cubital index, body size and character ratios of *A. koschevnikovi* from northern Borneo (n = 12) and southern Kalimantan (n = 30).

	South		North				
Characters	Mean	S.D.	Mean	S.D.	t-value	df	*P*-value
fem (5)	2.439	0.030	2.450	0.018	-1.16	40	0.2541
tib (6)	3.140	0.042	3.140	0.026	0.05	40	0.9634
ltar (7)	2.027	0.042	2.048	0.019	-1.66	40	0.1052
wtar (8)	1.102	0.023	1.091	0.014	1.60	40	0.1180
lt3 (9)	1.995	0.031	2.032	0.026	-3.62	40	0.0008*
lt4 (10)	1.923	0.034	1.961	0.029	-3.36	40	0.0017
lst3 (11)	2.657	0.037	2.612	0.057	2.99	40	0.0048
lwm (12)	1.106	0.031	1.053	0.027	5.22	40	0.0000*
wwm (13)	2.103	0.039	2.068	0.032	2.79	40	0.0080
dwm (14)	0.290	0.026	0.314	0.036	-2.37	40	0.0228
lst6 (15)	2.271	0.036	2.272	0.031	-0.08	40	0.9389
wst6 (16)	2.585	0.073	2.618	0.082	-1.27	40	0.2110
lfw (17)	8.534	0.113	8.492	0.130	1.04	40	0.3047
bfw (18)	2.972	0.040	2.984	0.041	-0.93	40	0.3596
cubital a (19)	0.581	0.026	0.574	0.011	0.92	40	0.3645
cubital b (20)	0.096	0.013	0.084	0.012	2.76	40	0.0086
a4 (21)	32.070	1.190	32.600	1.545	-1.20	40	0.2390
b4 (22)	104.397	3.433	104.723	2.819	-0.29	40	0.7716
d7 (23)	90.072	1.777	91.169	1.996	-1.75	40	0.0885
e9 (24)	20.532	0.973	20.154	0.479	1.28	40	0.2086
g18 (25)	94.564	2.400	93.997	1.746	0.74	40	0.4630
j10 (26)	44.501	1.608	43.970	1.507	0.98	40	0.3321
j16 (27)	105.534	2.964	109.328	1.791	-4.13	40	0.0002*
k19 (28)	75.431	2.445	75.437	2.205	-0.01	40	0.9943
l13 (29)	15.400	1.046	15.232	1.719	0.39	40	0.6993
n23 (30)	84.287	2.599	85.792	2.403	-1.73	40	0.0913
o26 (31)	29.341	2.027	32.715	1.645	-5.12	40	0.0000*
cub index	6.162	1.092	6.929	1.030	-2.09	40	0.0433
leg	7.607	0.102	7.639	0.047	-1.02	40	0.3137
body size	3.918	0.064	3.992	0.054	-3.57	40	0.0009*
body size/leg	0.515	0.007	0.523	0.006	-3.32	40	0.0019
wtar/ltar	0.544	0.008	0.532	0.009	3.95	40	0.0003*
lwm/wwm	0.526	0.012	0.509	0.009	4.34	40	0.0001*
lst6/wst6	0.879	0.030	0.869	0.029	1.05	40	0.3013
bfw/lfw	0.348	0.003	0.351	0.004	-2.73	40	0.0094

Bonferroni adjustment: $\alpha^* = 0.05/35 = 0.0014$; * significant.

14.3% of the variation; PC 3, angles of venation A4 (21) and B4 (22) with component loadings 0.68 and 0.86 accounting for 9.0%; PC 4, cubital a (19) and angles of venation J10 (26) and K19 (28) with component loadings between 0.51 and 0.60 accounting for 8.6%; PC 5, angle of venation L13 (29); PC 6, angle of venation N23 (30); PC 7, size-related character (16); PC 8, size-related character (14) accounting for 7.8%, 5.9%, 5.4% and 3.8% of the variation, respectively. The eight principal components accounted for a total of 78.7% of the variation in the data.

A PC plot using the first and second PC scores showed two clusters with the colonies from localities in the south mainly in the upper half of the plot and colonies from the northern localities in the lower half (Fig. 2a). This

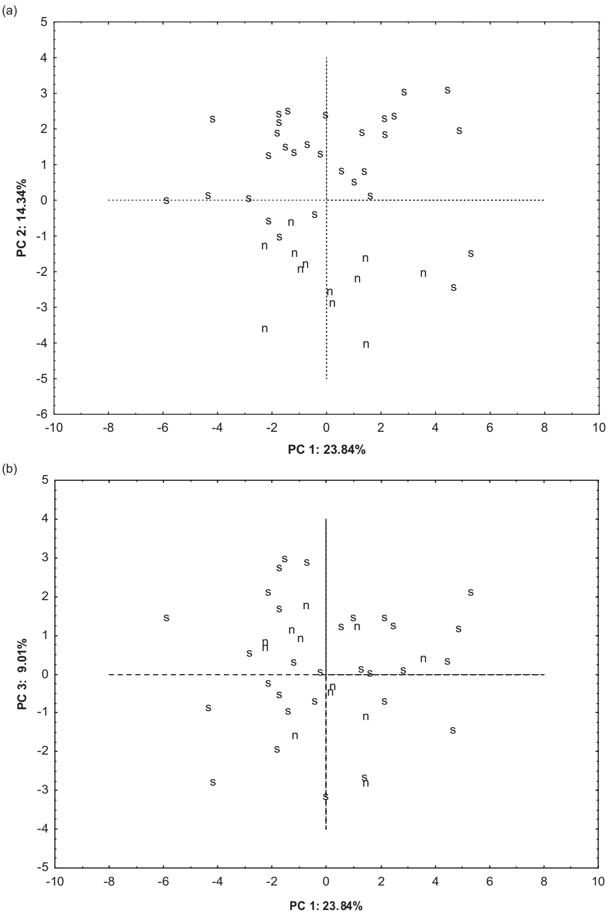

Figure 2. Principal components scores plots using the colony means of 27 morphometric characters of worker honeybees from southern Kalimantan (s) and northern Borneo (n). (a) PC 1 versus PC 2 scores; (b) PC 1 versus PC 3 scores.

indicates that for PC 2 there is a north/south cline mainly due to differences in the length of wax plate of sternite 3, (12) and the angle of venation O26 (31) (correlation: r = 0.61 for (12), r = 0.61 for (31), $P < 0.0001$). The PC plot for the first and third PC scores did not show a similar cline but revealed one morphocluster (Fig. 2b).

3.3. Analysis of combined Oberursel, Hadisoesilo-Raffiudin and Grahamstown databases

Principal components analysis was carried out on the morphometric databases of Oberursel, Hadisoesilo-Raffiudin and Grahamstown comprising colonies from Indonesia (Kalimantan and Sumatera), and Malaysia (Peninsula and Sabah), using the colony means of twelve morphometric characters of worker honeybees common to all the databases. Four principal components with eigenvalues greater than one were isolated: PC 1, size-related characters (5), (6), (7), (9), (10), (11), (15) and (17) with component loadings between 0.55 and 0.83 accounting for 36.5% of the variation; PC 2, size-related character (12) and angle of venation D7 (23) with component loadings 0.73 and 0.58, respectively, accounted for 18.6% of the variation; PC 3 and 4, angles of venation B4 (22) and G18 (25)

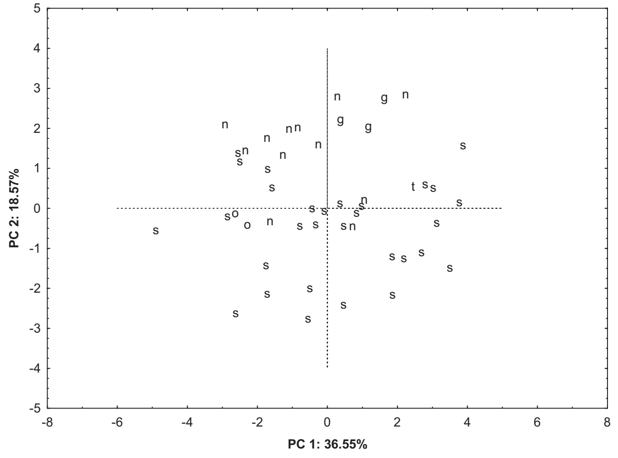

Figure 3. Principal components scores plots using the colony means of 12 morphometric characters of worker honeybees from southern Kalimantan (s), northern Borneo (Oberursel and (n), Grahamstown (g)), Malay Peninsula (o) and Sumatera (t).

with component loadings 0.60 and 0.82, respectively, accounted for 10.8% and 9.4% of the variation, respectively. The four principal components accounted for a total of 75.3% of the variation in the data.

PC plots using both the first and second PC scores again showed a cluster of colonies from southern Kalimantan and a cluster from northern localities from Sarawak and Sabah along the PC 2 axis (Fig. 3). A north/south cline was apparent in the PC 2 axis mainly due to differences in the length of wax plate of sternite 3, (12) (correlation: $r = 0.65$ for (12), $P < 0.0001$). New additional colonies from Long Semado (Borneo, n = 3) fell close to those from the northern localities, colonies from Ringlet (Malay Peninsula, n = 2) and the colony from Tanjungampalo (Sumatera, n = 1) fell close to those colonies from the southern localities. PC plots for the first and, third and fourth PC scores did not show a similar cline but revealed one morphocluster.

4. DISCUSSION

The multivariate analyses of the *A. koschevnikovi* samples clearly establish that this species is comprised of a single morphocluster. Moreover, the morphocluster can be delimited with as few as 12 morphological characters. It would also appear to be a very homogeneous species in comparison with *A. cerana* over the same area of distribution because the average coefficient of variation in *A. koschevnikovi* is 1.8% while in *A. cerana* it is 4.3% for the same 12 characters. *A. koschevnikovi* is often referred to in the literature as the "red bee of Sabah"; however "colour" was not used in our analyses because *A. koschevnikovi* is pale reddish in Sabah State, Borneo, Malaysia, but a dark, coppery colour in the Malay Peninsula and Sumatera, Indonesia (Otis, 1997).

The known geographical distribution of *A. koschevnikovi* is limited to the Malay Peninsula, Borneo, Malaysia and Borneo, Indonesia. The numerical weight of altitudinal distributions for *A. koschevnikovi* recovered from the literature provides values mostly below 1 200 m, but raises the question: is this because it is more difficult for collectors to reach higher elevations, or, are the bees actually scarcer there. Bearing in mind that the islands of the South China Sea were often connected to the mainland during much of the Pleistocene (Voris, 2000) and *A. koschevnikovi* occurs in tropical evergreen rain forests which extend into Thailand and Myanmar to the west and Cambodia and Vietnam to the east, its absence from the later appears puzzling at first sight.

However, Hughes et al. (2003) found a significant transition between northern Indochinese and southern Sundaic (Indomalay) avifauna assemblages just north of the Isthmus of Kra in the Thai–Malay peninsula. This area is associated with a change from wet seasonal evergreen dipterocarp rain forest to mixed moist deciduous forest north of the Isthmus of Kra. They also reviewed the climatological and ecological factors associated with the forest types and hypothesized that the avian transition tracks the northern phytogeographical boundary and that hypothetical seaways at the end of the Oligocene could account for the development of both phytogeographical and avifaunal transitions as well. To the extent that these interpretations are sound, they would very conveniently explain why *A. koschevnikovi* does not occur in tropical evergreen rain forests which extend into Thailand, Myanmar, Cambodia and Vietnam.

It is apparent that the range of *A. koschevnikovi* is diminishing because it is now either poorly represented or absent in several areas from which it has been previously recorded decades ago. This has been attributed to habitat changes resulting from deforestation and the establishment of tea, oil palm, rubber and coconut plantations (Otis, 1997; Eltz, 2004). A final point of interest is that throughout its range *A. koschevnikovi* is sympatric with *A. cerana*; however, the former is a denizen of the primeval evergreen rain forests of Sundaland while the latter can be abundant in agricultural and even urban settings.

Analyse morphométrique et biogéographie d'*Apis koschevnikovi* Enderlein (1906).

***Apis koschevnikovi* / morphométrie / aire de répartition**

Zusammenfassung – Morphometrische Analyse und Biogeographie von *Apis koschevnikovi* Enderlein (1906). An Arbeiterinnen von *Apis koschevnikovi* aus deren gesamten Verbreitungsgebiet in Südostasien wurden multivariate morphometrische Analysen durchgeführt. Siebenundzwanzig morphologische Merkmale der Arbeiterinnen wurden nach der Methode von Ruttner (1988) vermessen, die verwendeten Merkmale enthielten Größenmessungen und Flügelwinkel. Hieraus wurden acht Hauptkomponenten abgeleitet, die insgesamt 78,7 % der Variation in den Daten repräsentierten. Die multivariaten Analysen der Proben von *A. koschevnikovi* zeigten klar, dass die Art aus einem einzigen anhand von nur 12 morphologischen Merkmalen abgrenzbaren Morphokluster zusammengesetzt ist.

Die Hauptkomponentenanalyse zeigte einen die Bienen von Sumatra, Borneo und der malayischen Halbinsel enthaltenden Morphokluster (Abb. 2 und 3). Die Population ist einheitlicher als die von *A. cerana* in dem gleichen Verbreitungsgebiet. Dies kann aus dem Vergleich der mittleren Varianzkoeffizienten von 12 gleichen Merkmalen ersehen werden, der bei *A. koschevnikovi* 1,8 %, bei *A. cerana* aber 4,3 % beträgt.

Die Höhenverteilung zeigt, dass von den 102 erfassten Fundorten von *A. koschevnikovi* 96 % niedriger als 1200 m und 4 % zwischen 1200 und 2700 m lagen (Tab. I und zusätzliches elektronisches Onlinematerial zur Verteilung von *A. koschevnikovi* auf Grundlage aller publizierter Nachweise). Diese Höhenverteilung ist nicht unterschiedlich von der sympatrischen *A. cerana* (χ^2 = 6,9, df = 3, P = 0,0764). Sie ist aber signifikant verschieden von der Höhenverteilung der geographisch sympatrischen *A. nuluensis*, für die bisher nur drei Fundorte bekannt sind, die alle über 3000 m liegen (χ^2 = 104,0, df = 3, P < 0,0001).

In zahlreichen Exkursionen im tropischen Regenwald über die letzten 10 Jahre in Thailand, Myanmar, Kambodscha and Vietnam konnte die Art *A. koschevnikovi* nicht nachgewiesen werden, ihr Vorkommen ist auf die Region des immergrünen Regenwaldes von Sundaland begrenzt (Abb. 1). Anscheinend ist das Verbreitungsgebiet von *A. koschevnikovi* im Schwinden, da diese in einigen Gebieten, in denen sie früher gefunden wurde, nun nur geringfügig vertreten ist oder vollständig fehlt.

***Apis koschevnikovi* / Morphometrie / Verbreitungsgebiet**

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Online Material

Appendix I. Distribution of localities, co-ordinates, altitude (m) of *A. koschevnikovi* based on all published records. * Indicates localities where data are available, n = number of colonies.

Country & State/Province		Locality	Latitude	Longitude	Altitude	n
BRUNEI						
1		Bukit Sih	4.52N	114.55E	0	
2		Belalong Field station	4.43N	115.04E	74	
INDONESIA						
3	Kalimantan	Bettotan	5.49N	118.07E	0	
4	Sumatera	Geumpang	4.56N	96.09E	650	
5	Kalimantan	Long Pa Sia	4.22N	115.43E	1050	
6	Sumatera	Gunung Leuser Natl Park	3.46N	97.12E	8	
7	Kalimantan	Tanahmerah	3.40N	117.31E	8	
8	Sumatera	Bohorok	3.30N	98.12E	115	
9	Sumatera	Tambunan	3.27N	98.19E	161	
10	Sumatera	Sibaulangit	3.19N	98.34E	450	
11	Kalimantan	Kasai	2.13N	117.52E	0	
12	Kalimantan	Pelawanbesar	1.10N	117.54E	14	
13	Kalimantan	Kariorang	0.49N	117.52E	0	
14	Kalimantan	"Tabang, Bengen River"	0.34N	116.01E	125	
15*	Sumatera	Tanjungampalo	0.22N	102.32E		1
16	Sumatera	Muaralembu	0.24S	101.20E	128	
17	Kalimantan	Samarinda	0.30S	117.09E	50	
18	Sumatera	Pariaman	0.37S	100.07E	21	
19	Sumatera	Tanjunggampalu	0.37S	100.52E	224	
20	Sumatera	Muara	0.40S	100.57E	345	
21	Sumatera	Trawas	1.02S	102.47E	141	
22	Kalimantan	Gunung Palung Nat Park	1.13S	110.07E	655	
23	Kalimantan	Pan Kalan Kasai	1.15S	110.05E	500	
24	Kalimantan	Balikpapan	1.16S	116.49E	0	
25	Sumatera	Pelewan Mountain	1.36S	105.52E		
26	Kalimantan	Timpah	1.42S	114.25E	127	
27	Kalimantan	Lampung	1.48S	115.04E	65	
28	Kalimantan	Ketapang	1.50S	109.59E	30	
29	Sumatera	Muara near Solok	1.55S	100.52E	9	
30*	Kalimantan	Jungkal	2.20S	115.25E	23	4
31*	Kalimantan	Murung Jambu	2.31S	115.25E	25	1
32*	Kalimantan	Abung	2.31S	115.27E	80	1
33*	Kalimantan	Barabai	2.34S	115.22E	101	4
34	Sumatera	Surulangun	2.35S	102.47E	313	
35*	Kalimantan	Haliyau	2.38S	115.26E	50	2
36	Kalimantan	Kandangan	2.46S	115.16E	59	
37*	Kalimantan	Hulu Muka	2.49S	115.17E	14	5
38*	Kalimantan	Panggungan	2.49S	115.24E	100	1
39*	Kalimantan	Lumpage	2.49S	115.25E	134	2
40*	Kalimantan	Jelatang	2.50S	115.18E	28	1
41	Sumatera	Taboali	3.00S	106.30E	207	
42	Kalimantan	Tanahmerah Pulau	3.02S	116.10E		
43*	Kalimantan	Benua Lama	3.02S	115.58E	30	1
44*	Kalimantan	Berangas	3.14S	116.13E	29	3

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Country & State/Province		Locality	Latitude	Longitude	Altitude	n
45*	Kalimantan	Tirawan	3.14S	116.15E	72	1
46	Kalimantan	Banjarbaru	3.25S	114.49E	23	
47*	Kalimantan	Kersik Putih	3.29S	115.59E	35	2
48*	Kalimantan	Serakaman	3.29S	116.21E	45	2
49	Kalimantan	Lampake	3.34S	115.49E	1	
50	Sumatera	Bengkulu	3.47S	102.16E	8	
51	Sumatera	Cabang Research Station	4.39S	105.49E	1	
52	Sumatera	Goenoeng Tanggamoes	5.25S	104.42E	1000	
53	Sumatera	Bandar Lampung	5.32S	105.02E	575	
54	Java	Bangka	6.15S	106.49E	26	
55	Java	Tjimandala Gunung Pantjar	6.34S	106.54E	575	
56	Java	Tjibunar	6.49S	106.04E	57	
57	Java	Tjidaoen	7.28S	107.20E	29	
58	Java	Bukit Lawang	7.49S	112.42E	453	
59	Java	Kacangan	7.58S	111.40E	497	
MALAYSIA						
60	Sabah	Kudat	6.52N	116.49E	0	
61	Peninsula	Alor Setar	6.07N	100.22E	0	
62	Sabah	Kamburongoh	6.01N	116.32E	2673	
63	Sabah	Kota Kinabalu	5.58N	116.04E	8	
64	Sabah	Sepilok	5.52N	117.58E	180	
65	Sabah	Sandakan	5.49N	118.07E	0	
66	Sabah	Kerokot	5.49N	116.30E	786	
67	Sabah	Bukit Kretam	5.48N	118.59E	150	
68	Peninsula	Gunung Jerai	5.47N	100.04E	1000	
69	Sabah	Tambunan	5.47N	116.20E	1054	
70	Sabah	Kampong Kertam	5.31N	118.30E	80	
71*	Sabah	Tenom	5.07N	115.57E	500	9
72	Sabah	Deramakot	5.00N	117.00E	400	
73	Sabah	Danum Valley	4.95N	117.41E	100-1100	
74	Peninsula	Bukit Larut	4.47N	100.45E	109	
75	Sabah	Luasong	4.37N	117.24E	500	
76	Peninsula	Gunong Kledang	4.34N	101.01E	880	
77	Sarawak	Lambir Hills	4.28N	114.00E	80	
78	Peninsula	Gopeng	4.28N	101.10E	68	
79	Peninsula	Bertam Valley	4.25N	101.24E	1229	
80*	Peninsula	Ringlet	4.24N	101.22E	1135	2
81	Sarawak	Long Pa Sia	4.22N	115.43E	1050	
82	Sarawak	Miri	4.22N	113.58E	4	
83	Peninsula	Ayer Itam	4.16N	101.07E	15	
84*	Sarawak	Tawau	4.15N	117.54E	0	3
85*	Sarawak	Long Semado	4.15N	115.34E	858	3
86	Peninsula	Jerantut	3.55N	102.22E	108	
87	Sarawak	Mt Dulit	3.15N	114.15E	1238	
88	Peninsula	Bukit Kutu	3.12N	102.05E	804	
89	Peninsula	Kuala Lumpur	3.10N	101.42E	60	

Appendix I. Distribution of localities, co-ordinates, altitude (m) of *A. koschevnikovi* based on all published records. * Indicates localities where data are available, n = number of colonies.

Country & State/Province		Locality	Latitude	Longitude	Altitude	n
90	Peninsula	Dusun Tua	3.07N	101.49E	86	
91	Peninsula	Genting Highlands	3.06N	101.45E	1700	
92	Peninsula	Simpang Pertang	2.57N	102.16E	21	
93	Peninsula	Ayer Hitam	2.55N	102.24E	57	
94	Peninsula	Kampong Serting	2.49N	102.22E	80	
95	Peninsula	Kuala Pilah	2.43N	102.15E	98	
96	Peninsula	Melaka	2.12N	102.15E	1	
97	Sarawak	Balin Balai	2.04N	111.25E	28	
98	Sarawak	Matu	2.40N	111.31E	0	
99	Sarawak	Santubong	1.43N	110.17E	0	
100	Sarawak	Mt Matang	1.36N	110.10E	140	
101	Sarawak	Batu Kawa	1.31N	110.16E	15	
102	Sarawak	Tebakang	1.06N	110.30E	75	