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FURTHER NOTES ON THE SYSTEMATICS OF THE *ANOPHELES*  
*LEUCOSPHYRUS* GROUP (DIPTERA: CULICIDAE).

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IN a recent publication (Colless, 1956), to which the present paper forms a supplement, a general review was given of the systematics and biology of *Anopheles* "*leucosphyrus*"; i.e. the *A. leucosphyrus* species group. A major, and taxonomically quite distinct, member of the group, *A. leucosphyrus balabacensis*, was there awarded subspecific rank only, in view of its apparently allopatric distribution with regard to the type form, and the occurrence in Malaya of populations of a rather intermediate nature. These latter suggested the existence there of a zone of secondary integration between the two subspecies, and they were described under vernacular names as the "Fraser's Hill form" and the "Kepong form". However, in a footnote (Colless, *op. cit.*: 64), reference was made to recently acquired specimens which throw additional light on the status of the "Kepong form". Other collections have since been received, and it is the purpose of this paper to describe what appears to be the true situation, as revealed by this new material.

These recent collections comprise: (a) Three series of wild-caught females from jungle catches at Ulu Gombak, near Kuala Lumpur; (b) four series of adults, with correlated larval and pupal pelts, bred from eggs laid by single females from the same catches as (a) above; and (c) five series of adults, many with correlated larval and pupal pelts, reared from larval collections from around Kuala Lumpur and from Padang Besar, near the Thai border. For all these excellent series of specimens, I am deeply indebted to Lt.-Col. R. Traub of the U.S. Army Medical Research Unit, and Dr. J. A. Reid and Mr. Ganipathipillai of the Institute for Medical Research. I have also seen several useful series in the collections of the London School of Hygiene and Tropical Medicine and the British Museum (Natural History).

The first and most obvious fact revealed by these collections is the occurrence in Central Malaya of mixed populations of the "Kepong form" and *A. leucosphyrus leucosphyrus* (collections (a) and (b) above), in which there is no evidence whatsoever of morphological intergradation, every specimen being immediately recognisable as belonging to one or the other form—in collection (a), 20 specimens clearly belonged to the type form and 13 to the "Kepong form". The differences, moreover, involve a number of characters—in adult, larva, and pupa—and there is no suggestion of a balanced polymorphism, operating within a single species. This is to say, the morphological differences and sympatric occurrence show that the two forms belong to two different species.

Furthermore, in collection (b), the progeny raised from two females of *A. l. leucosphyrus* (33 and 29 adults respectively) and from two females of the "Kepong form" (25 and 13 adults) all bred true to their parent form in all characters, in all stages. Also, there is no indication of any abnormal degree

of variability in the "Kepong form", such as might be expected were hybridisation actually occurring. For instance, a sensitive differentiating character is the ratio of the lengths of pupal spines IV.A/III.A. Statistical analysis of various non-sibling series gave the following coefficients of variation (ratio of standard deviation to mean):—

<i>A. l. leucosphyrus</i> , Borneo, 10 specimens	. . . . .	23%
" " Malaya, 8 specimens	. . . . .	33%
<i>A. l. balabacensis</i> , Borneo, 11 specimens	. . . . .	24%
" " Malaya, 9 specimens	. . . . .	14%
" Fraser's Hill form", 10 specimens	. . . . .	18%
" Kepong form", 22 specimens	. . . . .	26%

The variable magnitude of these coefficients reflects nothing more than the number of batches from which the specimens were drawn, and the "Kepong form" and "Fraser's Hill form" show no sign of being intrinsically more variable than the others.

It is thus clear that the "Kepong form" is not a hybrid population, but genetically fixed and distinct, and the question arises to which species it should be allocated. As already noted (Colless, *op. cit.*), it bears marked resemblances to *A. l. balabacensis* in the key-characters for adult, larva, and pupa, and appears to be the Central Malayan representative of that form. I propose, therefore, to elevate *balabacensis* to specific rank and to treat the "Kepong form" as one of its subspecies. The specific rank of *balabacensis* is necessitated by the sympatric distribution of its terminal subspecies with the type form.

The recognition of *balabacensis* as a full species again raises the question of the necessity for further subspecific splitting, in the light of the geographic variation previously described (Colless, *op. cit.*). There is, in particular, the broad cleavage into forms, from the Asiatic mainland (excluding Central Malaya) and those from the Malaysian islands, based on several characters of the wing and the relative length of palp segments. However, since these differences are relatively slight—they would not fit within the "70 per cent. rule" of Mayr *et al.* (1953)—and since field workers would certainly not welcome further additions to the nomenclature, I see no necessity for any formal recognition of this subdivision.

There remains, however, the question of the three other variant forms, referred to as the "Negros", "Luzon" and "Fraser's Hill" forms (Colless, *op. cit.*). Of these, the "Negros form" is known only from a few specimens, and, although probably worthy of subspecific rank, analysis of further material would be required before any formal recognition could be granted. This applies also to the "Fraser's Hill form", which may be a distinct altitudinal subspecies or species, or a phenotypic variant produced by growth at high altitudes. The "Luzon form", however, has a number of very distinctive characters which clearly separate it from all others and, despite the few specimens available, I propose now to award it formal recognition.

Subspecific status would appear to be appropriate for this form, but there is some difficulty in choosing the species to which it should be allocated. Its larva is virtually identical with that of *balabacensis*, but the pupa closely resembles that of *leucosphyrus*. Also, the adult, although clearly separated from all other forms

by its pharyngeal teeth alone, tends to resemble *leucosphyrus* in its maxillary index, reduced tarsal banding, etc., but the same trend is found in the "Kepong form" of *A. balabacensis*. To add to the confusion, the key-character (the presector dark spot on wing vein 1) shows considerable variation, some specimens resembling *leucosphyrus* and some *balabacensis*. However, if geographical distribution is taken into account, it seems more logical to regard the "Luzon form" as derived from *A. balabacensis* (or, more probably, an undifferentiated parent stock), in parallel with *A. leucosphyrus*, which itself shows signs of having only recently become specifically distinct. I propose, therefore, formal recognition of the "Luzon form" as *A. balabacensis baisasi*, named in honour of Mr. F. E. Baisas, of the Philippine Department of Health.

As regards *A. balabacensis*, I have seen further specimens from near the Thai border (series (c) above) which agree with the form previously noted from that area, except that two variant females have the wing vein 1 with an abnormally long presector dark mark, resembling the condition typical of *A. l. leucosphyrus*. In all other characters, these specimens were typical of *A. balabacensis*. I have also seen several series from Taiwan (three larvae, three females, two males) in the collections of the London School of Hygiene and Tropical Medicine and the British Museum. These were all typical *A. balabacensis* except that, in the one specimen mounted, the maxillary index was abnormally high (16.0). There was no marked resemblance to the Philippine forms, except perhaps in the larvae, which had the palmate hairs very weakly developed on the metathorax and abdominal segment II.

Formal diagnoses of these new subspecies are given below, with a general outline of diagnostic characters for the *leucosphyrus-balabacensis* complex. Descriptions of the "Fraser's Hill form" and "Negros form", illustrations and full details of synonymy, are given in my previous paper (Colless, *op. cit.*). No reference is here made to the males, which in general resemble the females, but with a greater degree of variability which makes their identification of doubtful value. Quantitative data are summarised in Tables I-III.

*A. leucosphyrus* Dönitz, 1901.

Dönitz, W., 1901, *Insektenbörse* 18 : 37.

*Type locality* : SUMATRA : Kajoe Tanam.

*Type*: Co-type female in the British Museum (Natural History).

Adult female.

Wing with presector dark mark of vein 1 subdivided by pale spots (usually 3 or more) extending to, or almost to, the base of the vein; at least to the level of the base of the humeral dark mark of the costa. (Accessory sector pale spot usually extending to the costa on at least one wing; maxillary index about 17; pharyngeal teeth averaging about 15 in number; hind tarsal segment IV usually without any distinct basal pale band).

Larva.

Basal tubercles of the inner and central shoulder hairs usually not fused, that of the inner hair without any prominent apical tooth or spine. (Abdominal hair I.9 usually with 5 or more branches; hair IV.13 usually with 4 or more branches on both sides and about half as long as adjacent hair 12).

TABLE I.—*Adult characters: A. leucosphyrus and A. balabacensis.*

Form.	Number of specimens.	Ratios of palp segs.		Number of phar. teeth.	Maxillary index.	<sup>1</sup> Pre-sector dark mark, vein 1.	<sup>2</sup> Access. sect. pale spot, costa.	<sup>3</sup> Basal hind tarsal seg. IV.
		3/4.	3/5.					
<i>A. leucosphyrus</i> :								
Borneo	10	1.6-1.8 <i>1.69</i>	2.2-2.9 <i>2.60</i>	13-16 <i>14.7</i>	14-19 <i>16.9</i>	+++	14/16	1/16
Malaya	10	1.6-1.8 <i>1.69</i>	2.2-2.9 <i>2.59</i>	14-17 <i>15.6</i>	15-18 <i>16.7</i>	+++	65/72	14/63
Sumatra	1	1.65	2.38	?	?	+++	9/14	0/10
Overall	21	1.6-1.8 <i>1.69</i>	2.2-2.9 <i>2.59</i>	13-17 <i>15.2</i>	14-19 <i>16.8</i>	+++	88/102	15/89
<i>A. b. balabacensis</i> :								
N. Malaya	4	1.6-1.8 <i>1.68</i>	2.3-2.5 <i>2.35</i>	13-15 <i>14.0</i>	12-14 <i>13.0</i>	+, ++	0/12	12/12
Assam	3	1.5-1.6 <i>1.52</i>	2.2-2.4 <i>2.28</i>	14-15 <i>14.7</i>	13-15 <i>14.0</i>	+, ++	0/13	8/8
Burma	5	1.5-1.6 <i>1.55</i>	2.2-2.5 <i>2.33</i>	13-15 <i>13.6</i>	11-16 <i>13.0</i>	+, ++	0/12	12/12
<sup>3</sup> Asiatic mainland, miscell.	1	1.59	2.50	?	?	+, ++	0/9	9/9
Taiwan	1	1.65	2.52	16	11.5	+, =	0/4	4/4
Balabac	—					++	1/5	5/5
Borneo	10	1.6-1.9 <i>1.73</i>	2.4-2.9 <i>2.65</i>	12-15 <i>13.7</i>	11-15 <i>13.2</i>	=	61/100	100/100
Java	3	1.7-1.9 <i>1.80</i>	2.7-3.3 <i>2.93</i>	12-12 <i>12.0</i>	13-15 <i>14.0</i>	++	5/8	8/8
<i>A. b. introlatus</i>	14	1.4-1.8 <i>1.60</i>	2.3-3.0 <i>2.50</i>	12-19 <i>15.9</i>	15-18 <i>16.9</i>	+, =	47/56	13/53
<i>A. b. baisasi</i>	2	1.6-1.6 <i>1.60</i>	2.5-2.7 <i>2.60</i>	10-10 <i>10.0</i>	16-18 <i>17.0</i>	+, ++, +++	0/5	0/5
<sup>4</sup> <i>A. "leucosphyrus"</i> — "Fraser's Hill form"	6	1.6-1.7 <i>1.68</i> <i>1.61</i>	2.5-2.9 <i>2.70</i> <i>2.41</i>	16-20 <i>17.3</i>	16-18 <i>17.2</i>	=	0/9	5/9

Means are in italic figures.

<sup>1</sup> Basal extension relative to level of costal spots: = . . . corresponding with costal presector dark spot; + . . . to presector pale spot; ++ . . . to apical half of humeral dark spot +++ . . . to or past base of humeral dark spot (usual condition).

<sup>2</sup> Proportion of specimens seen to possess the character in question (numbers different from those in col. 1).

<sup>3</sup> Andamans—1 (palp measured); Thailand—1; Indo-China—3; Bengal—3; West India (Karwar)—1.

<sup>4</sup> Since it is not yet clear to which species this form belongs, the group name, in inverted commas, is used.

TABLE II.—*Larval characters* : *A. leucosphyrus* and *A. balabacensis*.

Form	Number of specimens.	Prothoracic hair 1.	Prothoracic hair 13.	Abdominal hair I.9.	Abdominal hair IV.13.
<i>A. leucosphyrus</i> :					
Borneo . . .	13	11-17, <i>14.1</i>	4-7, <i>6.2</i>	4-7, <i>5.4</i>	2-5, <i>3.9</i>
Malaya . . .	22	11-17, <i>13.2</i>	4-7, <i>6.5</i>	3-7, <i>4.9</i>	2-6, <i>4.2</i>
Overall . . .	35	11-17, <i>13.5</i>	4-7, <i>6.4</i>	3-7, <i>5.1</i>	2-6, <i>4.1</i>
<i>A. b. balabacensis</i> :					
N. Malaya . . .	10	11-22, <i>15.8</i>	3-7, <i>6.2</i>	3-5, <i>3.4</i>	2-4, <i>2.9</i>
Thailand . . .	6	14-24, <i>16.9</i>	4-7, <i>5.6</i>	3-5, <i>3.7</i>	3-4, <i>3.1</i>
Taiwan . . .	2	.	6-7, <i>6.8</i>	3-4, <i>3.3</i>	3-3, <i>3.0</i>
Balabac . . .	10	12-22, <i>15.2</i>	4-9, <i>5.6</i>	3-5, <i>3.7</i>	2-4, <i>2.9</i>
			(8 + in 2/10)		
Borneo . . .	30	10-21, <i>14.5</i>	4-7, <i>5.5</i>	3-5, <i>3.5</i>	2-4, <i>2.8</i>
Java . . .	15	11-21, <i>17.7</i>	5-8, <i>6.2</i>	3-5, <i>4.0</i>	3-4, <i>3.1</i>
			(8 in 2/15)		
<i>A. b. introlatus</i> . . .	36	10-21, <i>13.8</i>	5-11, <i>7.2</i>	3-7, <i>4.7</i>	2-5, <i>3.3</i>
			(8 + in 20/36)		
<i>A. b. baisasi</i> . . .	9	14-20, <i>16.6</i>	5-7, <i>5.8</i>	3-5, <i>3.6</i>	3-5, <i>3.3</i>
* <i>A. "leucosphyrus"</i> — "Negros form" . . .	3	15-20, <i>16.8</i>	4-7, <i>5.9</i>	3-5, <i>3.7</i>	3-3, <i>3.0</i>
* <i>A. "leucosphyrus"</i> — "Fraser's Hill form" . . .	10	15-23, <i>18.8</i>	6-10, <i>8.3</i>	3-6, <i>4.6</i>	3-4, <i>3.1</i>
			(8 + in 10/10)		

Means are in italic figures.

\* See footnote 4, Table I.

Pupa.

Ratios of lengths of lateral spines IV . A/III . A about 2.4, IV . A/V . A about 0.4. Toothed-margin index averaging 0.90 or more.

Distribution.

MALAYA : SUMATRA ; SARAWAK ; ? INDONESIAN BORNEO.

*A. balabacensis balabacensis* Baisas, 1936.

Baisas, F. E., 1936, *Philipp. J. Sci.* 59 : 65 (*A. leucosphyrus* var. *balabacensis*).

*Type locality* : PHILIPPINES : Balabac, Balabac Is.

*Types* : Male and female in Bureau of Health, Manila.

*Synonym* : *A. leucosphyrus balabacensis* (Colless, 1956).

Adult female.

Wing with presector dark mark of vein 1 subdivided by pale spots (usually 1-2), more or less corresponding in length with the presector dark mark of the costa, though in certain forms it may extend basally to about the level of the apical half of the humeral dark mark of the costa. (An accessory sector pale spot often present in the specimens from Borneo, Java and the Philippines, but not in those from the Asiatic Mainland or Taiwan. Maxillary index averaging about 12-14; pharyngeal teeth usually rather long and thin, 0.04-0.05 mm. in length, averaging about 14 in number, their apices not deeply

TABLE III.—*Pupal characters: A. leucosphyrus and A. balabacensis.*

Form.	Number of specimens.	Abdominal hair		Lateral spines, length in mm.			Lateral spines, ratios of lengths			Toothed-margin index.
		III·C.	IV·C.	III.	IV.	V.	IV/III.	IV/IV.		
<i>A. leucosphyrus</i> :										
Borneo	10	5-13, 7·5	3-8, 5·1	0·014	0·032	0·094	1·5-3·3, 2·34	0·2-0·5, 0·34	0·80-0·95, 0·89	
Malaya	21	3-8, 5·6	3-6, 4·6	0·015	0·043	0·095	1·6-4·0, 2·43	0·2-0·8, 0·42	0·87-0·96, 0·92	
<i>A. b. balabacensis</i> :										
N. Malaya	9	7-11, 9·0	5-10, 6·6	0·016	0·071	0·090	3·5-5·3, 4·40	0·7-0·9, 0·79	0·82-0·89, 0·85	
Balabac <sup>1</sup>	20	7-11, 8·3	5-8, 6·4	0·018	0·070	0·093	3·80	0·75	0·80 <sup>2</sup>	
Borneo	10	7-13, 9·0	5-9, 6·2	0·020	0·076	0·099	3·1-6·0, 3·99	0·7-0·9, 0·78	0·82-0·91, 0·88	
<i>A. b. introlatus</i>	38	5-13, 8·6	5-11, 7·5	0·023	0·087	0·109	2·3-8·0, 3·86	0·5-1·0, 0·80	0·84-0·95, 0·90	
<i>A. b. baisas</i> <sup>3</sup>	15	4-8, 5·4	3-4, 3·1	0·011	0·018	0·056	1·62	0·32	0·75-0·79, 0·77 <sup>3</sup>	
4A. " <i>leucosphyrus</i> ", "Negros form"	3	3-6, 4·5	3-5, 3·4	0·014	0·049	0·083	1·3-3·8, 2·83	0·3-0·6, 0·48	0·72-0·79, 0·75	
4A. " <i>leucosphyrus</i> ", "Fraser's Hill form"	10	5-11, 8·2	5-10, 6·3	0·018	0·047	0·118	2·0-3·2, 2·61	0·3-0·5, 0·40	0·80-0·89, 0·84	

Means are in italic figures.

<sup>1</sup> From Baisas (1936a and b) unless otherwise indicated.<sup>2</sup> From figure in Baisas (1936a).<sup>3</sup> From figure in Baisas (1936a), and two specimens measured.<sup>4</sup> See footnote 4, Table I.

dissected. Hind tarsal segment IV always with some indication of a basal pale band, this usually prominent.)

Larva.

Basal tubercles of the inner and central shoulder hairs usually fused, the inner one with a prominent apical tooth or spine. (Palmate hair of abdominal segment II usually with distinct lanceolate leaflets. Prothoracic hair 13 averaging about 5-6 branches, very rarely with 8 or more. Abdominal hair I.9 usually 3-4 branched; hair IV.13 almost invariably with only 2 or 3 spreading branches and distinctly more than half as long as adjacent hair 12. Pecten teeth not clearly differentiated into long and short types).

Pupa.

Hair III.C averaging about 8-9 branches, hair IV.C about 6. Ratio of lengths of lateral spines IV.A/III.A averaging about 3.8-4.4, of spines IV.A/V.A about 0.7-0.8. Toothed-margin index averaging 0.80-0.88.

Distribution.

INDIA (Karwar, Bengal, Assam); BURMA; THAILAND; MALAYA (near the Thailand border only); INDO-CHINA; ? HAINAN; TAIWAN; PHILIPPINES (Palawan and Balabac Is.); NORTH BORNEO; BRUNEI; SARAWAK (extreme north only); JAVA.

*A. balabacensis introlatus* subsp. n.

*Type locality* : MALAYA : Selangor, 15th mile Ulu Gombak.

*Types* : Holotype female and allotype male, with three female and two male paratypes, all with corresponding larval and pupal pelts; to be placed in the British Museum (Natural History).

*Synonym* : *A. leucosphyrus* "Kepong form" (Colless, 1956).

Differs from the type subspecies as follows :

Adult female.

(a) Wing usually with a costal accessory sector pale spot on at least one side (73/80 specimens).

(b) Maxillary index averaging about 17.

(c) Pharyngeal teeth averaging about 16 in number.

(d) Hind tarsal segment IV usually with minute basal pale band or none (a distinct band was seen in only 16/80 specimens).

Larva.

(a) Abdominal hair I.9 averaging about 5 branches (this number present on at least one side in 30/36 specimens).

(b) Prothoracic hair 13 averaging about 7 branches (8 or more present on at least one side in 20/36 specimens).

Pupa.

Lateral spines III.A and IV.A long, averaging 0.023 mm. and 0.087 mm., the longest in absolute size in the whole *leucosphyrus* group, though only a little longer than in the Borneo form of *A. b. balabacensis*.

Distribution.

Known only from the vicinity of the type locality.

*A. balabacensis baisasi* subsp. n.

*Type locality* : PHILIPPINES : Los Banos, Luzon Is.

*Type* : Holotype female to be placed in the British Museum (Natural History).

*Synonym* : *A. leucosphyrus*, "Luzon form" (Colless, 1956).

Differs from the type species as follows :

Adult female.

(a) Wing without any costal accessory sector pale spot ; presector dark spot on vein 1 variable, sometimes extending almost to the base of the vein.

(b) Hind tarsal segment IV without any distinct basal pale band. The banding of the fore tarsi is also rather reduced and does not completely encircle the segments, although this is difficult to see in old specimens.

(c) Maxillary index 16-18 (2 specimens).

(d) Pharyngeal teeth short and stout, length 0.03-0.04 mm. (2 specimens), their apices deeply dissected ; in general appearance resembling those of *A. riparis* rather than *A. balabacensis*. They are also few in number ; two specimens seen had 10 and Baisas (1936a) gives 8. (See illustrations in Baisas (1936a), and Colless (1956).

Larva.

(a) Palmate hair on abdominal segment II very weakly developed, hair-like or with barely flattened branches.

(b) Pecten with teeth clearly differentiated into long and short types.

Pupa.

(a) Lateral spine IV.A very short, averaging only 0.018 mm. ; ratio of lengths of spines IV.A/III.A about 1.6, of spines IV.A/V.A about 0.3 (these from the mean figures given by Baisas (1936b)).

(b) Hairs III.C and IV.C weakly branched, averaging about 5 branches and 3 branches respectively.

(c) Toothed margin index very low, less than 0.8 (3 specimens).

Distribution.

Known from the type-locality only.

#### DISCUSSION.

While the systematic position of *A. balabacensis introlatus* seems now to be well established, there remain several important problems for future investigation, in particular the questions of the identity of the "Fraser's Hill form" and of the junction between *introlatus* and the type subspecies. Unfortunately, there remains a large stretch of country, between the state of Selangor and the Thai border, from which I have no specimens at all of *A. balabacensis* ; it is clearly a matter of some importance to trace the transition, if any, between the two forms. This problem resembles that found in Borneo, where the actual boundary between *A. b. balabacensis* and *A. leucosphyrus* has not yet been delimited.

A noticeable feature of both *introlatus* and the "Fraser's Hill form" is the tendency to resemble the sympatric *A. leucosphyrus* in the number of pharyngeal teeth, the maxillary index, the reduced banding of hind tarsal segment IV, the presence of a costal accessory sector pale spot (in *introlatus* only), the short pupal spine IV.A (in the "Fraser's Hill form" only) and the branching of abdominal hair I.9 in the larva. That these resemblances have been introduced by hybridisation seems to be ruled out by present observations and general evolutionary theory, and the explanation must lie either in convergence, due to some direct or indirect adaptive significance attached to these characters, or in relic resemblance to a common ancestral form.

The course of evolution of these forms has been previously discussed (Colless, *op. cit.*), and it seems highly probable that *A. leucosphyrus* arose originally as an endemic species in Sumatra, subsequently re-colonising the Malay Peninsula. It has also been shown (Reid, 1950) that this latter area appears to possess certain peculiarities of environment, probably climatic and possibly involving rainfall distribution, which prevent the southward spread of a number of anopheline species (*A. minimus*, *A. ramsayi*, *A. annularis*, and *A. pallidus*) to which can now be added *A. b. balabacensis*. It seems probable, then, that the resemblances mentioned have been evolved by parallel adaptations to the Peninsula environment before and/or after the colonisation of Sumatra, and the return to Malaya of *A. leucosphyrus*. It is also possible, however, that the "*leucosphyrus*" which colonised Sumatra came from Malaya and still retains traces, adaptive or non-adaptive, of its original parentage.

Unfortunately, we have little precise information as to the finer details of the morphology of the Sumatran *A. leucosphyrus*, but there is one interesting batch of larval specimens (Colless, *op. cit.*: 82) which very likely belong to that form. These show a quite pronounced tendency to resemble *A. balabacensis* in several important features. This calls to mind the fact, discussed by Zeuner (1941) and Reid (1950), that in at least four groups of animals—reptiles, amphibia, butterflies, and mosquitoes—there are species whose distribution stops short at about the Malaya-Thailand border, but which re-appear in Sumatra. It seems, therefore, that the apparent peculiarities of the Malayan environment are absent from Sumatra and that those species which re-appear in Sumatra either traversed the Malay Peninsula before the appearance of such peculiarities, or came by some other route. One sees here some explanation for the above-mentioned resemblance between the Sumatran specimens and *A. b. balabacensis* and also a probability that the resemblances between *intro-latus* and the Malayan *leucosphyrus*, and the differences between the latter and the Sumatran form, are actually the result of convergent adaptation to the Malayan environment.

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